Optimization Model for Forest and Shrubland Birds

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Executive summary: The goal of this project was to inform forest management to balance the habitat needs of both mature-forest and shrubland birds means optimizing the amount and configuration of early- and mature-forest habitat needed. This was accomplished with a series of investigations consisting of 1) a review and meta-analysis of the published literature to quantify the response of both shrubland and mature forest birds to forest management, 2) the combination of functions describing these responses into an informal optimization model to identify forest practices that best accommodate both mature forest and shrubland birds, 3) the incorporation of these functions into an online decision support tool to permit users to visualize the effects of forest management on bird conservation.

 Our meta-analysis of literature on shrubland birds showed that of 21 species for which we had sufficient sample sizes for analyses, most (62%) exhibited monotonic declines of density with increasing tree retention, defined as percent basal area or canopy cover retained. Five other species (24%) exhibited quadratic relationships with tree retention. Finally, three additional species (14%) considered to be shrubland birds did not exhibit significant relationships with tree retention. In contrast, densities of 18 mature-forest bird species generally declined as tree retention and basal area decreased, although several forest bird species, such as wood thrush (*Hylocichla mustelina*) and yellow-bellied sapsucker (*Sphyrapicus varius*), had similar abundances among unharvested and partially harvested (e.g., shelterwood) stands, and others, like least flycatcher (*Empidonax minimus*) and eastern wood-pewee (*Contopus virens*), had their highest abundances in shelterwoods.

 Because any form of forest management favors some species over others, we weighted standardized, predicted individual species densities by Partners-in-Flight conservation values, and then summed these per-species weighted densities to generate an objective community-wide conservation index. We found that clearcuts and partially harvested stands typically had the highest conservation values due to their supporting both shrubland bird species of elevated conservation concern, but also mature forest species of conservation importance. We also conducted a meta-analyses of the effects of edges on nesting success and found that nest success for mature forest birds declines as nests are placed closer to edges, but no significant effect for shrubland birds.

 Finally we developed an online decision support tool provisionally named "Predictor of Avian Communities Tool", or PACT. At this point PACT only incorporates shrubland bird abundance conditioned on the geographic location, as well as patch size and time since treatment functions generated from previous CEAP supported research, along with the shrubland bird basal area retention relationships described above. Work is underway currently to incorporate the mature forest birds into the tool. Also included in the report is a discussion of the development process of this decision support tool including an evaluation of its functionality relative to published best practice recommendations. Together this report represents significant progress towards informing forestry practices in terms of the effects on bird communities by 1)

identifying exact tolerance limits of shrubland and mature forest birds to logging intensity (in the form of basal area retention), 2) summarizing the effects of logging on edge-related nest success, and 3), presenting these findings in an easily accessible format for non-specialists to access for guidance on management practices on their lands.

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I.   A meta-analysis of the effects of tree retention on shrubland birds

Summary: The effects of forest management on native fauna are of key interest to managers and conservationists. Individual studies have expanded our knowledge of management impacts, but meta-analyses of multiple studies are needed to summarize and integrate findings into a more generalizable form. Most meta-analyses on the effects of tree harvesting have focused on mature forest taxa because of concerns for these species; however, early-successional specialists, such as shrubland birds in the eastern United States, are also of key conservation concern. Using data from 34 studies that examined the effects of silvicultural treatments on bird communities, we conducted a meta-analysis to determine the effects of tree retention on a suite of bird species reported to be associated with shrubland habitats within the northeastern United States. Of 21 putative shrubland bird species for which we had sufficient sample sizes for analyses, most (62%) exhibited monotonic declines of density with increasing tree retention, defined as percent basal area or canopy cover retained. Five other species (24%) exhibited quadratic relationships with tree retention. Finally, three additional species (14%) considered to be shrubland birds did not exhibit significant relationships with tree retention. We also calculated density estimates of shrubland birds in three categorical classifications of basal area retention corresponding to common management regimes: regeneration harvests with little retention (clearcut and seed-tree methods), regeneration harvests with moderate retention (shelterwoods), and high retention management regimes (commercial thinning, selection methods, no management). Many of the shrubland species had high densities in clearcuts as well as in stands with low levels (5-25%) of mature tree retention, and some species had equally high densities in stands with moderate tree retention (30-70%), supporting the use of retention forestry approaches, which can provide other benefits associated with mature trees. Overall, our findings provide managers and conservationists with robust, quantitative relationships of shrubland birds with tree retention. Managers can use these quantitative relationships for more detailed planning and evaluation of silvicultural projects, more so than what was feasible using previous findings of shrubland bird responses to discrete silvicultural treatments from disparate studies.

Keywords: Avian, logging, review, silviculture, tree harvest, young forest

1. Introduction

Terrestrial wildlife communities are influenced by changes in vegetation structure and composition resulting from forest management (e.g., Webb et al., 1977; King and DeGraaf, 2000). Wildlife associated with mature, closed-canopy forests tend to decline in abundance when silvicultural harvests create more open-canopy conditions (Vanderwel et al., 2007; Semlitsch et al., 2009; Kalies et al., 2010; Tilghman et al., 2012). In contrast, other species increase in abundance in forest stands with intermediate levels of overstory tree canopy and understory vegetation density resulting from light- to mid-intensity tree harvests (Sheehan et al., 2014; Perry et al., 2018). Finally, open-canopy, shrubland specialists favor a shrubby, dense understory with few overstory trees, and are typically most abundant after high-intensity tree harvests (Freedman et al., 1981; Baker and Lacki, 1997; Kendrick et al., 2015).

Our understanding of bird and wildlife responses to tree retention is derived from individual studies conducted at discrete sites that typically compare abundance between mature closed-canopy forest and a few silvicultural treatments (e.g., Annand and Thompson, 1997; Goodale et al., 2009; Boves et al., 2013), as well as meta-analyses that synthesize effects across sites and treatment intensities (e.g., Schiek and Song, 2006; Vanderwel et al., 2007; Zwolak,

2009; Kalies et al., 2010; Tilghman et al., 2012; Fontaine and Kennedy, 2012; Vershuyl et al., 2011; Fedrowitz et al., 2014; Twedt, 2020). Meta-analyses are highly useful in quantitatively integrating findings across many studies (Arnqvist and Wooster, 1995); however, previous meta-analyses on tree harvesting have mainly focused on mature forest species or species richness and biodiversity (Vershuyl et al., 2011; Fedrowitz et al., 2014; LaManna and Martin, 2017). The focus of meta-analyses on overall biodiversity and closed-canopy forest species under-appreciates early-successional and open-canopy forests and their associated species.

        Worldwide, naturally regenerating, early-successional habitats are under-valued from a conservation perspective (Swanson et al., 2011), and few meta-analyses on the effects of silviculture have focused on these early-successional wildlife communities. Most management regimes still emphasize rapid development towards closed canopy forest conditions, even though prolonged periods of open forest conditions following disturbance are increasingly being recognized as ecologically important (Donato et al., 2012; Hanberry and Thompson, 2019; Palik et al., 2020). Several regions, such as eastern North America, contain a higher proportion of early-successional, shrubland bird specialists that are threatened and in need of conservation action and targeted management compared to mature forest species (Dettmers, 2003; King and Schlossberg, 2014).

        Eastern North America is an exception to the worldwide focus on mature forests, as the vulnerability of open-canopy habitats and shrubland birds in this region has received more emphasis in the past few decades (Hunter et al., 2001; Thompson and DeGraaf, 2001). Historically, these open habitats were created and maintained by natural disturbances, including beaver activity and associated flooding, as well as Native American burning regimes before European colonization (Askins, 2000). In the 19th and 20th centuries, abandoned agricultural fields also became a source of shrubland habitat (Lorimer and White, 2003). However, fire and flooding are currently suppressed, and abandoned fields have grown into middle-aged forests that are less susceptible to wind throw compared to the original old-growth forest stands (Litvaitis, 2003; Nowacki and Abrams, 2008; Shifley et al., 2014). Correspondingly, an increasingly large body of research has been generated on the effects of forest management to create habitat for birds that use young seral stages in eastern North America (King et al., 2011a; King and Schlossberg, 2014), but variability among sites, treatments, survey methods, and species compositions limit the general applicability of individual studies. Studies have found that shrubland birds decline in abundance in stands with increased tree basal area or canopy cover, although the strength of this relationship may differ among species and locales (Annand and Thompson, 1997; King and DeGraaf, 2000; Vanderwel et al., 2007; Smetzer et al., 2014). Furthermore, most studies analyze bird community response as a function of discrete management categories, whereas changes in bird community composition are more accurately characterized along a gradient of tree retention (Annand and Thompson, 1997; Vanderwel et al., 2007; Twedt, 2020). Thus, there is a great need for synthesized information to provide management guidance on the effects of silvicultural harvests on shrubland birds.

        We conducted a meta-analysis on shrubland birds of the northeastern United States, to provide a quantitative assessment of species-specific responses to tree retention levels along a gradient of stand conditions, from clearcut harvests to unmanaged forest. Since information on the effects of discrete silvicultural prescriptions are also useful for planning, communication, and comparison with other studies, we also examined shrubland bird densities as a function of three common management regimes: regeneration harvests with low retention (clearcut and seed-tree methods), regeneration harvests with moderate retention (shelterwoods), and lastly, high

retention management regimes (commercial thinning, selection methods, no management). Our meta-analysis provides synthesized information to forest managers on how shrubland bird densities respond to tree harvesting practices, both along a continuous gradient of tree removal and at discrete intervals. Managers can use this information in the course of their planning and evaluation activities to understand the potential impact of proposed or planned practices on shrubland species at any given retention level in a forest stand.

2. Methods

2.1. Literature search

We searched the literature for articles pertaining to the effects of tree harvesting on breeding shrubland birds in eastern North America. In May-August 2018, we searched Google Scholar and Web of Science databases, with the following search terms: "bird", and/or "avian", and "residual tree", "green tree retention", "shelterwood", "single-tree selection", "thinning", "seed-tree", "clearcut", "regenerating forest", or "timber harvest", with some additional searches also including "shrubland", "young forest", "early-successional", or "eastern United States" (Lott et al., 2019). We also used backward and forward 'snowballing' techniques to search for suitable studies (Wohlin, 2014). For instance, we examined article 'Cited by' lists in Google Scholar, as well as reference lists within studies, including reference lists from similar meta-analyses (Vanderwel et al., 2007; Verschuyl et al., 2011; Fontaine and Kennedy, 2012). We searched for any relevant peer-reviewed publications, unpublished theses and dissertations, and government technical reports. After reviewing manuscript titles and/or abstracts on search engines, we downloaded a total of 105 manuscripts to examine further.

2.2. Inclusion criteria

We further screened the potential studies using a number of inclusion criteria. Given that we were primarily interested in examining relationships of shrubland birds of northeastern North America, we only included studies that were conducted in southeastern Canada or the eastern United States, including USFS region 8, which extends from Texas and Oklahoma east to Florida and Virginia, and region 9, which extends from Missouri to Minnesota east to Delaware and Maine. While some eastern shrubland bird ranges extend to western North America or north into the boreal forest, examining basal area relationships for shrubland birds in forest types outside of eastern North America was beyond the scope of our study. To be included, studies needed to present either bird density estimates, or abundance data that could be standardized by unit area, for at least two northeastern shrubland bird species of interest, defined as bird species listed in Schlossberg and King (2007). Consistent with similar meta-analyses (Vanderwel at al., 2007; Kalies et al., 2010), we did not include single-species studies, which may have had different survey methods (e.g., mapping color-banded birds) and could have introduced publication bias into our study (Gurevitch and Hedges, 1999).

We included studies with a variety of different tree harvests, including single-tree selection, tree thinning, shelterwood, retention harvest, even-aged reproduction (EAR), seed-tree, and clearcuts. We also included studies with group selection cuts (e.g., Robinson and Robinson, 1999; Holmes et al., 2004), as long as they were less than 0.5 ha (range = 0.05-0.4 ha), because openings of this size would be interspersed throughout a stand. We did not include studies with group selection cuts between 0.5-1 ha, as we were often uncertain of the proportion of bird surveys that were conducted within these larger openings or in the adjacent, unharvested forest. We included studies that surveyed birds in clearcuts if the treated stands were >1 ha, as clearcuts

<1 ha may have lower abundance due to patch size (Chandler et al., 2009; Shake et al., 2012; Roberts and King, 2017).

We only included studies that examined bird abundance in harvested stands <16 years since treatment, as most shrubland birds typically decline in abundance in stands older than 15-20 years (Schlossberg and King, 2009). All included studies had at least some managed stands between 0-10 years since treatment (Table 1). We did not analyze time since treatment because studies often present averaged bird abundances across a range of stands with varying years since treatment. Furthermore, we could not assign a year since treatment value for abundance of birds in mature forest stands. Relationships with years since treatment have been reported elsewhere in other studies (Keller et al., 2003; Perry and Thill, 2013), including at least one meta-analysis (Schlossberg and King, 2009). We excluded studies that had canopy cover loss due to fire or other natural disturbances, and studies in tree plantations, which have inherently different management regimes than naturally regenerating forests (Iglay et al., 2018).

Almost all the studies that we included in our analysis contained information on the forest characteristics in control and treated stands, such that we could determine the tree retention levels in the treated stands (Vanderwel et al., 2007). Within each study, we primarily used the ratio of the mean basal area of treated stands versus the control mature forest stands to compute the percent tree retention level in the treated stands. All mature forest stands were classified as having 100% tree retention. The percent tree retention values were highly correlated with basal area values ($n = 51$, $r = 0.93$; Appendix A: Fig. A.1a). If the study omitted basal areas, we used percent canopy cover to determine the tree retention level, or in rare cases, we used other quantifiable metrics (Vanderwel et al., 2007). Canopy cover values were also highly correlated with percent tree retention ($n = 36$, $r = 0.86$; Appendix A: Fig. A.1b). As an exception, we also included studies in clearcuts ($n = 7$) which did not have vegetation and/or bird abundance data in both treated areas and in unmanaged forest stands (e.g., Thompson et al., 1992; King et al., 2009), because sample sizes for this treatment type were limited. If the study did not mention any residual trees in the clearcut stands, we assigned a 0% retention level. Alternatively, if the study mentioned that the clearcuts contained small numbers of residual trees, we assigned a 10% tree retention level (which was approximately the mean tree retention level for studies with clearcuts that had basal area data).

Meta-analysis studies can have bias because of the 'file drawer effect,' in which proportionally more published papers that contain significant results are included in the analysis, compared to unpublished studies that may lack significant results (Arnqvist and Wooster, 1995; Gurevitch and Hedges, 1999). We do not foresee a 'file drawer effect' in our meta-analysis, as we included both published manuscripts and unpublished theses. Additionally, forest retention studies are readily published irrespective of significant differences in bird abundance between control and treatment stands because lack of significant results are equally useful to managers and conservationists (e.g., Weakland et al., 2002; Otto and Roloff, 2012). Furthermore, all of the included studies examined the effects of forest retention on multiple bird species in a community-based approach and studies included species-level data regardless of significant differences between control and treated stands. We did not examine if effect sizes in our study were biased (Gurevitch and Hedges, 1999) because we were not directly examining effect sizes in our analyses (see statistical analysis below). Regardless, we have no reason to believe publication bias would occur in our type of study (Kalies et al., 2010; Fontaine and Kennedy, 2012).

2.3. Data extraction

For each study, we recorded the study's location, survey method, area of the forest stands, forest type, shrubland bird species, raw mean abundance or density and their standard errors (SEs) for each species in mature forest and treated sites, time since treatment for treated sites, and values of tree retention (mean basal area, canopy cover, and/or other metrics). Most studies had data presented in tables, but for a handful of studies we used Web Plot Digitizer Version 4.1 (Rohatgi, 2018) to obtain bird and/or tree retention data from figures. The majority of studies (68%) had bird abundance data in unmanaged control stands and in treated stands with just one level of tree retention. A smaller number of studies had unmanaged stands and treatment stands with multiple tree retention levels (n = 9, 26%), and a few studies (n = 2, 6%) only had data from clearcuts (Table 1). In a given study, we included the abundance or density of a given shrubland bird species if the species had an abundance >0 in either treated or mature stands.

After recording the raw mean abundance or density and their standard errors in mature forest and harvested stands for each species within a study, we standardized all avian data to the number of birds/ha. Some studies did not have density data, but instead presented mean abundance per point count. For these data, we recorded the point count circle radius (e.g., 40m, 50m, 75m), and divided the mean abundance by the circle area to convert the data to a standardized density estimate. Four studies used unlimited-distance point counts and for these studies we assumed a 75m radius to obtain standardized density values (i.e., abundance values per point divided by 1.77). We used a 75m radius for these unlimited-distance counts because detection probability of most species likely declines past 50m (Schieck, 1997; Reidy et al., 2011; Newell et al., 2013), and density values standardized by a 75m radius appeared to be more reasonable and similar to estimates from other studies, in comparison with standardizing with a 100m radius (dividing abundance values by 3.14).

2.4. Statistical analysis

We conducted a regression-type meta-analysis (Schlossberg and King, 2009), using primary data of mean densities of shrubland birds recorded in forest stands with different tree retention levels, rather than using effect sizes, response ratios, or relative abundance indices in our analyses (Hedges et al., 1999; Kalies et al., 2010; Tilghman et al., 2012). Common meta-analytical approaches using effect sizes and metrics such as Hedges' d or Cohen's d are calculated with sample sizes and standard deviations (Hedges et al., 1999), yet many relevant studies did not present these data. Moreover, determining the true sample size in forest biodiversity studies is difficult (Hurlbert, 1984; Spake and Doncaster, 2017), because bird surveys at point or transect locations were often conducted multiple times within a year and among years, and were often replicated within the same stand or forestry block. To circumvent the lack of sample sizes and standard deviations, previous studies on the effects of retention forestry on wildlife have computed meta-analyses with relative abundance indices or response ratios, rather than using effect sizes (Vanderwel et al., 2007; Kalies et al., 2010; Tilghman et al., 2012). However, response ratios were not viable for our study because shrubland birds often have negligible abundance in mature forest stands; therefore, treated stands have unmeasurable relative increases in abundance compared to control stands. Moreover, clearcut stands could not be defined as the baseline/control retention level, because most relevant studies in the literature did not examine bird abundance in clearcut and partially harvested stands, but rather compared abundance in harvested stands with mature forest controls.

We therefore chose to examine standardized mean density data for separate tree retention levels in each study, account for variation among studies using mixed-effects models (Gurevitch

and Hedges, 1999), and use the standard errors of bird density to weight the data in our regression analyses (Vanderwel et al., 2007). Our approach was a viable alternative because we effectively standardized the density data among studies, and most studies included standard errors for each mean density estimate per species. To compute a weight for each bird density data point, we divided the SE by the mean density, and then standardized this weight to a value ranging between 1 and 2 (multiplying by -1 and adding 2 to all SE/mean values; Vanderwel et al., 2007). As a result, in our regression analyses, data with higher weights had relatively smaller standard errors compared to data with lower weights. In some tree retention levels within studies, mean bird densities were 0, and we could therefore not compute a real-number SE/mean weight for these data. For these density values of 0, we conservatively inputted the lowest real-number weight computed for the other retention level(s) in the same study for that given species (Vanderwel et al., 2007). We also chose to include data from studies that did not present standard errors, although this was a small subset (n = 4, 12%) of the total included studies. For these studies that lacked standard errors, we set each bird density value to a weight of 1, the lowest weight for a sample in our analyses, given that we were uncertain of the precision of the data from these studies.

2.4.1. Continuous effect of tree retention analysis. We fit Generalized Linear Mixed Models (GLMM) separately for each species with at least 15 data points. We used bird density as the response variable, the percentage of trees retained as the main, continuous predictor variable, and included a random effect of study. The random effect accounted for different sampling methods and survey designs among studies, while also accounting for interdependence of data points in studies with multiple levels of tree retention (Fontaine and Kennedy, 2012). We used weighted regression models, in which each data point was weighted by the computed weight values described above. We fit the models using Gamma distributions with a log link, because the density data were non-negative, non-integers, and were often right-skewed (Bolker, 2008). We added a small number of 0.1 to all bird densities in order to be able to fit data values of 0 to Gamma distributions. Exploratory tests examining residual mean square errors, mean absolute errors, and figures with predicted curves and observed values showed that adding 0.1 to the data provided good model fits for the various species compared to adding a small value of 0.01, 0.001, or 0.0001 (Kalies et al., 2010).

We ran three models for each species: a null model depicting constant density (without the predictor variable), a model with a linear predictor of tree retention, and a model with a quadratic and linear predictor of tree retention. We examined models with quadratic relationships because we assumed there might be more complex relationships for some species based on the findings of prior studies (Annand and Thompson, 1997). We used an information-theoretic approach to compare the three models for each species, comparing values of Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). For two species, dark-eyed junco and magnolia warbler, one of the three mixed-effect models run per species did not converge, likely because of small sample sizes. For these two species, we compared AIC_c values using simpler, fixed-effect models without the random effect of study. We defined the top model for each species as the model with the lowest AIC_c value, if the difference in AIC_c from the top model to the next highest supported model (ΔAIC_c) was greater than 2 (Arnold 2010). If there were multiple models within 2 ΔAIC_c values, we chose the most parsimonious model (i.e., the one with the fewest parameters) as our top model in order to avoid extra, uninformative parameters (Arnold, 2010). After model selection, the top mixed model with

the random effect converged for all the species, so model parameters and significance values were presented from mixed-effects models.

2.4.2. Discrete treatments analysis. In addition to examining a continuous effect of tree retention, we also were interested in comparing bird densities among discrete, categorical levels of silvicultural treatments. We first assigned each basal area value within a study to a treatment type classification based on forest-type-specific basal area recommendations in the literature for different regeneration methods and management regimes (Table 2). Thus, given the forest type and mean basal area of the treatment level within a study, we denoted the treatment level as a regeneration harvest with low retention, regeneration harvest with moderate retention, or a high retention stand. For low retention stands, we binned basal area values lower than shelterwoods (e.g., seed tree systems) with clearcuts, including clearcuts with reserves. Moderate retention stands were defined as shelterwoods (Table 2). High retention was defined as stands with higher basal area values than shelterwoods: unmanaged forest, basal area values consistent with uneven-aged management (e.g., single-tree selection), and commercial thinning regimes. We chose to bin treatment levels into only three categories because of the small sample sizes for some species and to assist in model convergence. Some studies only presented canopy cover and not basal area, and in these cases, we used the percent forest retained value to compute an estimated basal area value, based on a function between known basal areas and percent forest retained observed in other studies (Appendix A: Fig. A.1a). We then used this predicted basal area value to place the treatment level within the study into one of our three binned categories.

We conducted similar weighted Generalized Linear Mixed Models (GLMM), fit to Gamma distributions, separately for each species to examine categorical levels of treatment types. As before, we used bird density as the response variable, and now included a main categorical predictor variable with three retention levels: low, moderate, and high. GLMMs did not converge for five species (American goldfinch, American robin, dark-eyed junco, indigo bunting, and yellow-breasted chat), and we used simpler, fixed-effect models without the random effect of study for these species. All analyses were conducted in the R statistical program version 3.4.3 (R Core Team, 2017), and we used the lme4 and lmerTest packages to conduct mixed-effect models (Bates et al., 2015; Kuznetsova et al., 2016), and the ggeffects package for plotting predictions (Lüdecke, 2018).

3. Results

We included 34 studies in our meta-analysis (Table 1), and acquired adequate data (>14 density estimates) to fit models for 21 species. Based on AIC_c values, most species (86%) had support for either a monotonic or quadratic relationship between tree retention and bird density (Table 3). The null model was the top model for three species (black-and-white warbler, dark-eyed junco, and yellow-billed cuckoo; see Table 3 for scientific names), and thus there was little support for a relationship between bird density and tree retention for these species (Appendix A: Fig. A.2).

Models with a single linear predictor of tree retention received the most support for 13 species: American goldfinch, American robin, brown-headed cowbird, Carolina wren, cedar waxwing, common yellowthroat, eastern towhee, magnolia warbler, northern cardinal, prairie warbler, ruby-throated hummingbird, white-eyed vireo and white-throated sparrow (Table 3). The strength of the relationship between the tree retention gradient and bird density varied among these thirteen species (Table 4, Fig. 1). Three of the species: northern cardinal, American robin, and Carolina wren, had weak relationships with tree retention (Fig. 1). The random effect

of study accounted for 59-77% of the variation in the mixed models for these three species, and post-hoc, fixed-effect models, without the random effect of study, were not significant (P > 0.1).

Models with a linear and quadratic predictor variable of tree retention received the most support for five species: chestnut-sided warbler, gray catbird, indigo bunting, mourning warbler and yellow-breasted chat (Table 3). These five species had more complex relationships with tree retention, with a decline of bird density only when greater than 40-50% of the trees were retained (Table 5, Fig. 2).

Examining densities among the three discrete treatment levels, brown-headed cowbird, cedar waxwing, common yellowthroat, chestnut-sided warbler, eastern towhee, ruby-throated hummingbird and white-throated sparrow had the greatest densities in regeneration harvests with low retention, significantly lower densities in shelterwoods (moderate retention) compared to stands with low retention, and lowest densities in high retention stands (Table 6). Carolina wren, gray catbird, indigo bunting, magnolia warbler, mourning warbler, prairie warbler, white-eyed vireo and yellow-breasted chat were equally abundant in low-retention harvests and shelterwood cuts, and less abundant in high retention stands compared to either low retention or shelterwoods. Northern cardinal and American goldfinch were significantly more abundant in shelterwoods than high retention stands, but abundance was not significantly different in low-retention versus high retention stands, and in low-retention versus shelterwood cuts. Finally, American robin, black-and-white warbler, dark-eyed junco and yellow-billed cuckoo did not differ among any of the discrete treatment levels.

4. Discussion

Using data from studies across eastern North America, our meta-analysis illustrates that shrubland bird abundance declines with tree retention along a continuous gradient, consistent with individual studies that have compared only a few discrete tree retention levels at relatively small geographic scales (e.g., King and DeGraaf, 2000; Goodale et al., 2009). In addition to high densities in complete clearcuts, numerous shrubland species had high densities in stands with low levels of mature tree retention (5-25%), lending support to retention forestry (Gustafson et al., 2012; Otto and Roloff, 2012; Grinde et al., 2020). Overall, our results across studies can be applied to specific, proposed management scenarios, to specify the level of basal area or tree retention that provides habitat for specific shrubland bird species.

The association of the shrubland bird guild with open canopy conditions and their absence from closed canopy forest has led some investigators to conclude that silvicultural treatments that retain a low level of canopy retention are the most efficient for conserving these species (King and DeGraaf, 2000; DeGraaf and Yamasaki, 2003). Our observation that most shrubland species decreased monotonically with tree retention supports this view — (i.e., 13 of 21 species, 62%, were best fit with a linear predictor) — which has also been borne out by field investigations in specific landscapes (e.g., Smetzer et al., 2014). Nevertheless, we also found several species were equally abundant in forest stands with 25-50% tree retention as they were in stands with 0-25% tree retention, consistent with findings on some individual species (Harrison and Kilgo, 2004; Roth et al., 2014; Margenau et al., 2018). Some shrubland bird species likely respond favorably to silvicultural treatments that mimic natural disturbance conditions, including wind events and ice storms that leave remnant standing trees singly or in groups (Faccio, 2003; Holmes et al., 2004). Moreover, some shrubland birds may be adapted to the partially-open, woodland conditions historically associated with oak and pine forests in portions of the eastern United States prior to the suppression of historic fire regimes (Hanberry and Thompson, 2019).

The association of shrubland birds with recently disturbed sites is clearly due to changes in vegetation structure and composition. Herbaceous growth and low, woody vegetation are less developed under conditions of greater tree retention, and characteristics of the herb and shrub layer influence the presence and abundance of shrubland bird species (Keller et al., 2003; Schlossberg et al., 2010). Many shrubland birds nest, forage, and hide from predators in or under shrubs, grasses, or herbaceous forbs and ferns (Schlossberg et al., 2010; Akresh, 2012; Greenlaw, 2020). As fewer trees are retained and basal area decreases in a stand, the amount of sunlight increases, and subsequently the understory vegetation is enhanced and can support insect prey, afford suitable nests sites, and can promote concealment from nest and post-fledging predators (Annand and Thompson, 1997; Smith et al., 1997; Akresh et al., 2009). Shrubland birds are likely responding to these changes in ecological conditions and vegetation structure resulting from silvicultural treatments.

Besides needing dense understory vegetation, shrubland birds may be using retention trees within harvested areas, or closed-canopy forests adjacent to clearcuts, for singing, foraging, and other behaviors (Akresh and King, 2016; McNeil et al., 2018). Roth et al. (2014) speculated that golden-winged warblers (*Vermivora chrysoptera*) were associated with some retained canopy because trees provide elevated singing posts to broadcast their songs. Other shrubland bird species, like the chestnut-sided warbler, forage extensively in closed-canopy forests adjacent to openings (Roberts and King, In Press) and females make forays into the forest to collect bark from birch (*Betula* spp.) trees for nest-building (King, Pers. Obs.), suggesting that retained trees can afford additional values to shrubland birds in managed stands (Grinde et al., 2020). We note that our analyses could not incorporate treatment area, and a small amount of retention throughout the stand may be especially important for shrubland birds in very large (e.g., >50 ha) harvested stands where there is less mature forest edge (Roth et al., 2014).

To our knowledge, Vanderwel et al. (2007) is the only other meta-analysis to examine individual bird species responses to silviculture as a continuous function of tree retention in North America; however, that study focused on mature forest birds and only included seven putative shrubland species. Their findings for five of these species were similar to ours: indigo buntings, white-throated sparrows, brown-headed cowbirds, and American robins increased with canopy removal and black-and-white warbler abundance was unrelated to canopy retention. In contrast to our results, Vanderwel et al. (2007) found dark-eyed juncos increased in response to canopy removal, whereas juncos were found to be unaffected by tree retention in our study. Lastly, Vanderwel et al. (2007) observed mourning warblers were unaffected by tree retention, whereas they increased with tree removal in our study.

Black-and-white warbler, dark-eyed junco and yellow-billed cuckoo were not influenced by tree retention in our study, despite being considered shrubland birds in at least some classifications (DeGraaf and Yamasaki, 2001; Hunter et al., 2001). Unlike other species that are virtually never present in the absence of open-canopy conditions, these three species appear more variable in their response to silviculture (King and DeGraaf, 2000; Rodewald and Yahner, 2000; Goodale et al., 2009; Otto and Roloff, 2012). Habitat features needed by these three species likely vary independently from silvicultural treatments. Both black-and white warblers and juncos are ground nesters, and for these species, suitable nesting sites might be less likely to be affected by silvicultural treatments than for birds that nest in shrubs or trees. Schlossberg and King (2007) attempted to generate a list of species that should be considered shrubland birds by calculating the percentage of studies in which a given species was more abundant in shrubland habitat, and black-and-white warbler, dark-eyed junco and yellow-billed cuckoo all had

relatively low values for this index (≤ 0.64), whereas species that exhibited a significant relationship in our study with tree retention typically had higher values (mean $= 0.83$). The variability in response to silviculture by these three species suggests they should not be generally considered shrubland species, although they might be associated with disturbance in certain systems.

Unsurprisingly, most of the species that we found to exhibit significant relationships with a continuous gradient of tree retention also differed among discrete silvicultural categories in our analyses. Specifically, cedar waxwing, common yellowthroat, eastern towhee, ruby-throated hummingbird, and white-throated sparrow had the highest densities in low retention harvests, then shelterwoods, then high retention stands, and also were best fit with a single linear predictor variable of tree retention. All of these species except cedar waxwings are widely considered shrubland species (Schlossberg and King, 2007). Species similarly abundant in low retention harvests and shelterwoods, and also best fit with a quadratic model, consisted of gray catbird, indigo bunting, mourning warbler, and yellow-breasted chat. These species are also widely considered shrubland birds, given that the shrubland bird designation is typically made in the context of abundance in treated stands relative to unmanaged forest (e.g., Schlossberg and King, 2007). Several other species exhibited monotonic relationships with our continuous variable, yet were still equally similar between the low retention harvests and shelterwood discrete categories (Carolina wren, magnolia warbler, prairie warbler and white-eyed vireo). Our continuous variable was based on percent tree retention, while our discrete silvicultural categories were based on shelterwood basal-area classifications, which can vary depending on the forest type. These slight differences in classifications may explain our varied results for these latter four species. All four species exhibited some higher density values around 50% retention, which, despite the strong monotonic relationship with the continuous variable, were enough to obscure the differences we expected in the discrete, categorical analysis.

We were unable to robustly analyze the effects of tree retention for shrubland bird species which were detected in relatively few primary studies. Nevertheless, exploratory examinations of some other putative shrubland bird species that had small sample sizes, such as song sparrow (*Melospiza melodia*), blue-winged warbler (*Vermivora cyanoptera*), and alder flycatcher (*Empidonax alnorum*), suggested similar declining densities as tree retention increased (Akresh unpublished data), consistent with previous knowledge of these species' habitat requirements (Arcese et al., 2020; Gill et al., 2020). Highly threatened shrubland species such as golden-winged warblers were not detected in the community-based studies we examined in our meta-analysis, but other studies that have focused on golden-winged warblers have observed highest abundances in basal areas between 0-12 m^2/ha (Leuenberger et al., 2017; McNeil et al., 2018).

The goal of our analyses was to identify conditions suitable for breeding birds in managed forests, however these findings are based only on abundance, and do not necessarily reflect habitat quality as manifested by bird survival and reproductive success (Van Horne, 1983). Brown-headed cowbirds are a brood parasite that can decrease the nesting success of host bird species, and we found cowbirds increase in abundance with decreasing canopy retention. Our results on cowbird abundance are consistent with the findings of others (Annand and Thompson, 1997; Vanderwel et al., 2007), and raise the possibility that decreased basal retention could potentially compromise bird nesting success in some landscapes. Cowbird abundance and brood parasitism can be especially detrimental in landscapes with extensive agricultural development (Robinson et al., 1995). Nevertheless, cowbirds tend to be scarce and cowbird parasitism low in extensively forested landscapes (Annand and Thompson, 1997; King and

DeGraaf, 2000; Chandler et al., 2009; King et al., 2009), and shrubland birds may be able to endure impacts of low levels of parasitism via re-nesting and other mechanisms (Smith, 1981; Guigueno and Sealy, 2010; Akresh, 2012). Similarly, nest predator abundance is not typically elevated by silviculture in extensively forested landscapes (King et al., 1996; King and DeGraaf, 2000; Chandler et al., 2009). Thus, landscape context may be important when considering tree harvests and potential impacts on bird productivity.

4.1. Conclusion and management implications
Nearly all shrubland bird species were less abundant or absent from forests with high levels of canopy cover, including unmanaged forests, single-tree selection, and commercial thinning regimes, and we therefore do not recommend these practices for shrubland bird management. Based on our findings, we believe that maximizing shrubland bird abundance in any given landscape can be achieved through four potential approaches: 1) creation of open-canopy (<30 %) early-successional forests via regeneration harvests, 2) short-rotation maintenance of open-canopy habitats, 3) creation of partially open-canopy (30-70%) forests via silviculture, and where appropriate 4) maintenance of partially open-canopy woodlands in fire-dependent ecosystems via prescribed burning and other practices (King and Schlossberg, 2014; Hanberry and Thompson, 2019).

As expected, regeneration harvests such as clearcuts and seed tree harvests were most efficient for creating habitat for shrubland birds. Historically, solely even-aged regeneration methods, such as clearcutting, have been suggested as strategies for creation of early-successional forest on commercial lands with high site quality (Hanberry and Thompson, 2019). Our results highlight that many shrubland bird species still attain high densities in areas where there is some low-level retention, suggesting that variable retention harvest systems maintaining live-tree legacies at densities below 25% may be an effective strategy for shrubland birds while also providing other benefits associated with large tree habitats (Fedrowitz et al., 2014; Mori and Kitagawa, 2014; Soler et al., 2016). Conditions created by retention forestry approaches more likely approximate natural post-disturbance conditions (Gustafsson et al., 2012). The habitats created through these regeneration methods will be ephemeral, but can exist throughout a landscape in a shifting mosaic or patch dynamic framework, with spatially distinct areas providing shrubland bird habitat at different times (DeGraaf et al., 2005; Akresh et al., 2015). Non-silvicultural, human-made habitats maintained with a dense understory and with few trees can also sustain large populations of shrubland birds. Maintained shrublands include wildlife openings, uncultivated land on small-scale farms, utility rights-of-way, and reclaimed surface mines (King and Schlossberg, 2014; Schlossberg and King, 2015).

Partially-open canopy conditions also provided habitat for shrubland birds, suggesting shelterwood methods and woodland restoration efforts may be used to conserve these species, especially if these stands are extensive throughout the landscape (Vander Yacht et al., 2016). Similar to low retention harvests, shelterwoods could be located on operational forests with high site quality. Shelterwoods also tend to be ephemeral in providing shrubland bird habitat, but two or three-stage shelterwoods, followed by a regenerating harvest (clearcut), could prolong habitat at a given site (Margenau et al., 2018). Alternatively, restoration and maintenance of partially-open-canopy oak-pine woodlands on low-quality, non-commercial xeric sites, maintained with low-intensity prescribed burning or other methods, could also provide habitat on a large scale (Brawn, 2006; Kabrick et al., 2014; Reidy et al., 2014). Given that some shrubland bird species have equal or higher abundance in stands with 30-70% canopy cover compared to 0-30% canopy

cover, and other shrubland species occupy stands with 30-70% canopy cover to some degree, partially-open stands could be a viable management option for helping to conserve shrubland birds.

Overall, our quantitative relationships can help balance the needs of shrubland birds with other forest values, such as 1) habitat for bird and wildlife species that require the retention of canopy trees for foraging or nesting (Vanderwel et al., 2007; Tilghman et al., 2012), 2) encouraging the regeneration of tree species that require some shading or a seed source for propagation (Smith et al., 1997), or 3) softening the appearance of silvicultural openings for recreationalists (e.g., Gobster, 1999). Balancing different values is aided by having our computed continuous functions between bird abundance and tree retention, because the functions should lend themselves more readily to generating management practices that may resolve these potentially conflicting values (Toms and Villard, 2005). We also note that a number of wildlife species that breed in mature forests, including mature-forest birds, still prefer open-canopy habitat during some stage of their life cycle, such as the post-fledging period (DeGraaf and Yamasaki, 2001; Akresh et al., 2009; Chandler et al., 2012). Therefore, we suspect that many different forest and stakeholder values can be upheld by maintaining a small amount of tree retention in silvicultural harvests, and by sustaining a variety of harvest intensities, seral stages, and management approaches throughout a regional landscape.

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Table 1. Studies included in the meta-analysis examining tree retention levels and shrubland bird abundance in Eastern North America.

Study	Location	Survey type	Survey area	Years since treatment	Retention levels	Forest Type
Annand and Thompson, 1997	MO	10-min Pt Count	unlimited	3 to 6	15, 55, 78, 78, 100	O-H
Atwell et al., 2008	MN	Transects	5 ha	3	50, 100	RP
Baker and Lacki, 1997	KY	12-min Pt Count	50m	1 to 2	0, 11, 26, 100	O-H
Boardman and Yahner, 1999	PA	5-min Pt Count	30m	1 to 5	27, 100	NH-M
Doyon et al., 2005	QC	10-min Pt Count	60m	9 to 12	85, 100	NH-M
Duguid et al., 2016	CT	12-min Pt Count	50m	1 to 7	44, 100	NH-M
Fink et al., 2006	MO	Spot mapping		3 to 5	10	O-H
Flaspohler et al., 2002	MI	10-min Pt Count	50m	2 to 10	81, 100	NH
Freedman et al., 1981	NS	Spot mapping		3 to 5	0, 51, 100	NH
Goodale et al., 2009	CT	12-min Pt Count	75m	1 to 16	40, 89, 100	NH-M
Greenberg et al., 2014	NC	Transects	0.875 ha	0 to 2	39, 100	O-H
Hache et al., 2013	NB	Spot mapping		4	69, 100	NH
Hagan et al., 1997	ME	10-min Pt Count	50m	1 to 5	10, 100	NH
Harrison and Kilgo, 2004	SC	Transects	50m	2	0, 100	BH
Heltzel and Leberg, 2006	LA	10-min Pt Count	unlimited	1 to 5	67, 100	BH
Holmes et al., 2012	ON	5-min Pt Count	50m	5 to 7	54, 56, 70, 100	NH
Holmes et al., 2004	ON	Transects	2 ha	2 to 6	54, 68, 100	NH
Jobes et al., 2004	ON	10-min Pt Count	unlimited	1 to 5	54, 100	NH
Kendrick et al., 2015	MO	Spot mapping		3 to 5	10, 100	O-H
King and DeGraaf, 2000	NH	10-min Pt Count	50m	3 to 5	4, 68, 100	NH
King et al., 2009	MA	10-min Pt Count	50m	4 to 7	10	NH
King et al., 2011b	MA	10-min Pt Count	50m	1 to 4	45, 100	PPSO
Margenau et al., 2018	AL	Spot mapping		2	6, 46, 50, 100	O-H
McDermott and Wood, 2009	WV	10-min Pt Count	50m	6 to 11	0, 100	NH
Newell and Rodewald, 2012	OH	Transects	200m long	1 to 3	44, 100	O-H
Perry and Thill, 2013	OK/AR	10-min Pt Count	40m	5	40, 59, 100	O-H S
Rankin and Perlut, 2015	VT	10-min Pt Count	50m	1 to 3	82, 100	NH-M
Robinson and Robinson, 1999	IL	6-min Pt Count	50m	2 to 3	68, 100	NH
Rodewald and Yahner, 2000	PA	10-min Pt Count	50m	2 to 6	21, 100	O-H

Thatcher, 2007	TN	Spot mapping		1 to 4	71, 100	O-H
Thompson et al., 1992	MO	Transects	500m x 75m	1 to 10	10, 100	O-H
Tozer et al., 2010	ON	5-min Pt Count	unlimited	2	75, 100	NH
Wilson et al., 1995	AR	8-min Pt Count	40m	1 to 14	68, 100	O-H S
Ziehmer, 1993	MO	Transects	50m	1	76, 100	O-H

Forest type abbreviations: BH = Bottomland Hardwoods, NH = Northern Hardwoods, NH-M = Northern Hardwoods-Mixedwoods, O-H = Oak-Hickory, O-H S = Mixed Oak-Hickory Shortleaf Pine, PPSO = Pitch Pine-Scrub Oak, RP = Red Pine.

Table 2. Classifications of shelterwood treatments, given the residual basal area and forest type. We used these shelterwood classifications when analyzing bird densities among discrete treatment categories.

Forest type	Shelterwood Basal Area (m^2/ha)	Sources
Northern hardwoods	6.9-18.4	Leak et al., 2014
Oak-hickory (central hardwoods)	13.8-20.7	Gingrich, 1971; Johnson et al., 2009
Northern hardwoods-mixedwoods	6.9-18.4	Leak et al., 2014
Pitch pine-scrub oak	4.6-11.5	New Jersey Pinelands Commission, 2006
Bottomland hardwoods	11.5-18.4	Gilmore and Palik, 2006
Mixed oak-hickory shortleaf pine	9.2-18.4	Larsen et al., 2010; Mahaffey and Evans, 2016
Red pine	9.2-18.4	Kabrick et al., 2007

Table 3. Model comparisons of a null, linear, or quadratic relationship between tree retention and bird density for each shrubland species, fit with Gamma distributions in Generalized Linear Mixed Models. Models were compared using values of Akaike's Information Criterion corrected for small sample sizes (AIC_c). For each species, we defined the top model as the model with the lowest AIC_c value, if the difference in AIC_c from the top model to the next highest supported model (ΔAIC_c) was >2. If multiple models were <2 ΔAIC_c, indicating similar support, we defined the simplest model (i.e., Null or Linear) as the top model.

Species	ΔAIC_c Null	ΔAIC_c Linear	ΔAIC_c Quad	Top Simplest Model
Black-and-white warbler (*Mniotilta varia*)	0.72	0.77	0	Null
Dark-eyed junco (*Junco hyemalis*)	0.00	2.96	3.84	Null
Yellow-billed cuckoo (*Coccyzus americanus*)	0.00	0.80	5.45	Null
American goldfinch (*Spinus tristis*)	11.2	0.00	4.11	Linear
American robin (*Turdus migratorius*)	6.74	0.018	0.00	Linear
Brown-headed cowbird (*Molothrus ater*)	52.1	0.26	0.00	Linear
Carolina wren (*Thryothorus ludovicianus*)	4.40	1.74	0.00	Linear
Cedar waxwing (*Bombycilla cedrorum*)	29.9	0.00	1.09	Linear
Common yellowthroat (*Geothlypis trichas*)	77.9	0.00	1.26	Linear
Eastern towhee (*Pipilo erythrophthalmus*)	87.4	0.00	2.24	Linear
Magnolia warbler (*Setophaga magnolia*)	7.86	0.00	1.20	Linear
Northern cardinal (*Cardinalis cardinalis*)	8.23	0.00	2.81	Linear
Prairie warbler (*Setophaga discolor*)	50.8	0.00	2.97	Linear
Ruby-throated hummingbird (*Archilochus colubris*)	20.8	0.00	2.54	Linear
White-eyed vireo (*Vireo griseus*)	21.5	0.00	0.91	Linear
White-throated sparrow (*Zonotrichia albicollis*)	35.2	0.82	0.00	Linear
Chestnut-sided warbler (*Setophaga pensylvanica*)	80.4	7.14	0.00	Quadratic
Gray catbird (*Dumetella carolinensis*)	27.3	5.56	0.00	Quadratic
Indigo bunting (*Passerina cyanea*)	121.5	19.5	0.00	Quadratic
Mourning warbler (*Geothlypis philadelphia*)	46.0	23.9	0.00	Quadratic
Yellow-breasted chat (*Icteria virens*)	92.0	15.1	0.00	Quadratic

Table 4. Sample size (n), the number of studies included, percent of the model variance accounted for by the random effect of study, model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate) and their SEs in parentheses, t values, and p-values for shrubland bird species in which the top model included the linear predictor of tree retention. The percent of the variance accounted for by the random effect of study was computed by dividing the variance of the random effect with the total variance in the model (the variance of the random effect plus the residual variance; Zuur et al. 2009). Species are listed in order of the strength of the model, based on the t value.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	t	p
Common yellowthroat	26	11	0.562	0.336 (0.234)	-2.298 (0.139)	-16.6	<0.001
Eastern towhee	40	17	0.595	0.389 (0.218)	-2.010 (0.139)	-14.5	<0.001
Prairie warbler	28	12	0.472	0.056 (0.257)	-2.377 (0.229)	-10.9	<0.001
Brown-headed cowbird	34	13	0.564	0.216 (0.269)	-1.762 (0.190)	-9.3	<0.001
White-throated sparrow	21	9	0.515	0.559 (0.315)	-2.499 (0.281)	-8.9	<0.001
Cedar waxwing	23	10	0.550	-0.451 (0.224)	-1.180 (0.151)	-7.8	<0.001
White-eyed vireo	19	7	0.384	-0.135 (0.296)	-2.046 (0.317)	-6.5	<0.001
Ruby-throated hummingbird	19	9	0.395	-1.154 (0.169)	-0.991 (0.157)	-6.3	<0.001
American goldfinch	17	8	0.266	-0.525 (0.275)	-1.429 (0.322)	-4.4	<0.001
Magnolia warbler	18	7	0.497	-0.721 (0.248)	-0.733 (0.187)	-3.9	<0.001
Northern cardinal	25	11	0.766	-0.790 (0.378)	-0.708 (0.194)	-3.7	<0.001
American robin	26	11	0.695	-0.683 (0.317)	-0.531 (0.158)	-3.4	0.001
Carolina wren	21	8	0.592	-0.513 (0.376)	-0.628 (0.253)	-2.5	0.013

Table 5. Shrubland bird species in which the top model also included a quadratic predictor of tree retention. Presented are the sample size (n), the number of studies included, the proportion of variance accounted for by the random effect of study, and model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate, β_2 = quadratic parameter estimate) and their SEs in parentheses.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	β_2 (SE)
Chestnut-sided warbler	42	18	0.399	0.355 (0.260)	0.044 (0.833)	-2.235 (0.689)
Gray catbird	21	9	0.631	-1.361 (0.287)	1.352 (0.731)	-2.023 (0.605)
Indigo bunting	54	23	0.529	-0.102 (0.206)	0.814 (0.627)	-2.637 (0.534)
Mourning warbler	24	10	0.358	-0.956 (0.256)	2.838 (0.804)	-4.222 (0.669)
Yellow-breasted chat	29	11	0.229	0.139 (0.183)	0.371 (0.707)	-2.854 (0.612)

Table 6. Effect of treatment type on shrubland bird density in forestry stands across the eastern United States. Values shown represent model-predicted mean density estimates per bird species and per treatment type, with 95% confidence intervals in parentheses. Low-retention harvests include any stands with basal areas less than shelterwoods, while high-retention forest includes any stands with basal areas greater than shelterwoods (see Table 2). Estimates with shared letter superscripts are not statistically different. Presented in the table header, we also used the raw basal area values from treatment levels within studies (n = 51), to compute a mean and SE of basal area for each of our discrete categorical treatment bins.

	Low retention harvests 5.6 m^2/ha (SE = 1.8)	Shelterwood (moderate retention) 15.7 m^2/ha (SE = 0.73)	High retention stands 24.7 m^2/ha (SE = 0.93)
Low retention > shelterwood > high retention			
Brown-headed cowbird	0.83^a (0.46-1.51)	0.48^b (0.28-0.81)	0.25^c (0.15-0.40)
Cedar waxwing	0.56^a (0.35-0.87)	0.40^b (0.26-0.63)	0.19^c (0.12-0.29)
Common yellowthroat	1.42^a (0.88-2.29)	0.38^b (0.24-0.59)	0.14^c (0.09-0.22)
Chestnut-sided warbler	1.71^a (1.05-2.80)	0.74^b (0.49-1.11)	0.19^c (0.13-0.28)
Eastern towhee	1.08^a (0.72-1.65)	0.41^b (0.26-0.64)	0.21^c (0.14-0.31)
Ruby-throated hummingbird	0.33^a (0.23-0.49)	0.18^b (0.13-0.25)	0.12^c (0.09-0.16)
White-throated sparrow	1.40^a (0.73-2.67)	0.60^b (0.31-1.14)	0.14^c (0.08-0.26)
Low retention = shelterwood > high retention			
Carolina wren	0.42^a (0.22-0.80)	0.74^a (0.36-1.52)	0.30^b (0.16-0.55)
Gray catbird	0.24^a (0.14-0.42)	0.32^a (0.20-0.52)	0.14^b (0.09-0.22)
Indigo bunting	1.09^a (0.77-1.56)	0.86^a (0.52-1.42)	0.25^b (0.18-0.35)
Magnolia warbler	0.43^a (0.27-0.70)	0.36^a (0.23-0.56)	0.22^b (0.15-0.34)
Mourning warbler	0.48^a (0.29-0.80)	0.50^a (0.33-0.75)	0.12^b (0.08-0.18)
Prairie warbler	0.55^a (0.33-0.90)	0.49^a (0.26-0.92)	0.11^b (0.07-0.18)
White-eyed vireo	0.35^a (0.21-0.56)	0.40^a (0.25-0.66)	0.11^b (0.07-0.17)
Yellow-breasted chat	1.20^a (0.78-1.86)	0.67^a (0.33-1.36)	0.16^b (0.10-0.25)
Shelterwood > high retention, low retention = high retention, low retention = shelterwood			
Northern cardinal	0.34^{ab} (0.16-0.69)	0.35^a (0.17-0.69)	0.25^b (0.13-0.50)
American goldfinch	0.31^{ab} (0.12-0.82)	0.46^a (0.26-0.83)	0.16^b (0.10-0.27)
Low retention = shelterwood = high retention			
American robin	0.31^a (0.10-0.91)	0.67^a (0.33-1.34)	0.38^a (0.22-0.66)
Black-and-white warbler	0.44^a (0.30-0.63)	0.32^a (0.21-0.47)	0.37^a (0.26-0.52)
Dark-eyed junco	0.34^a (0.15-0.78)	0.20^a (0.09-0.45)	0.33^a (0.17-0.63)
Yellow-billed cuckoo	0.14^a (0.08-0.26)	0.23^a (0.12-0.42)	0.17^a (0.10-0.30)

Figure 1. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the model with a linear predictor was the best fit. Grey lines and shading represent the weighted regression curves from the mixed models (fit to Gamma distributions) and 95% confidence intervals. Points indicate bird density values from individual studies, and larger points indicate that the data point had a higher weight in the model. To fit the models to Gamma distributions, all bird abundances had a small number of 0.1 added to them (so the lowest possible density was 0.1). COYE = common yellowthroat, EATO = eastern towhee, PRAW = prairie warbler, BHCO = brown-headed cowbird, WTSP = white-throated sparrow, CEDW = cedar waxwing, WEVI = white-eyed vireo, RTHU = ruby-throated hummingbird, AMGO = American goldfinch, MAWA = magnolia warbler, NOCA = northern cardinal, AMRO = American robin, CARW = Carolina wren.

Figure 2. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the quadratic model was the best fit. CSWA = chestnut-sided warbler, GRCA = grey catbird, INBU = indigo bunting, MOWA = mourning warbler, YBCH = yellow-breasted chat.
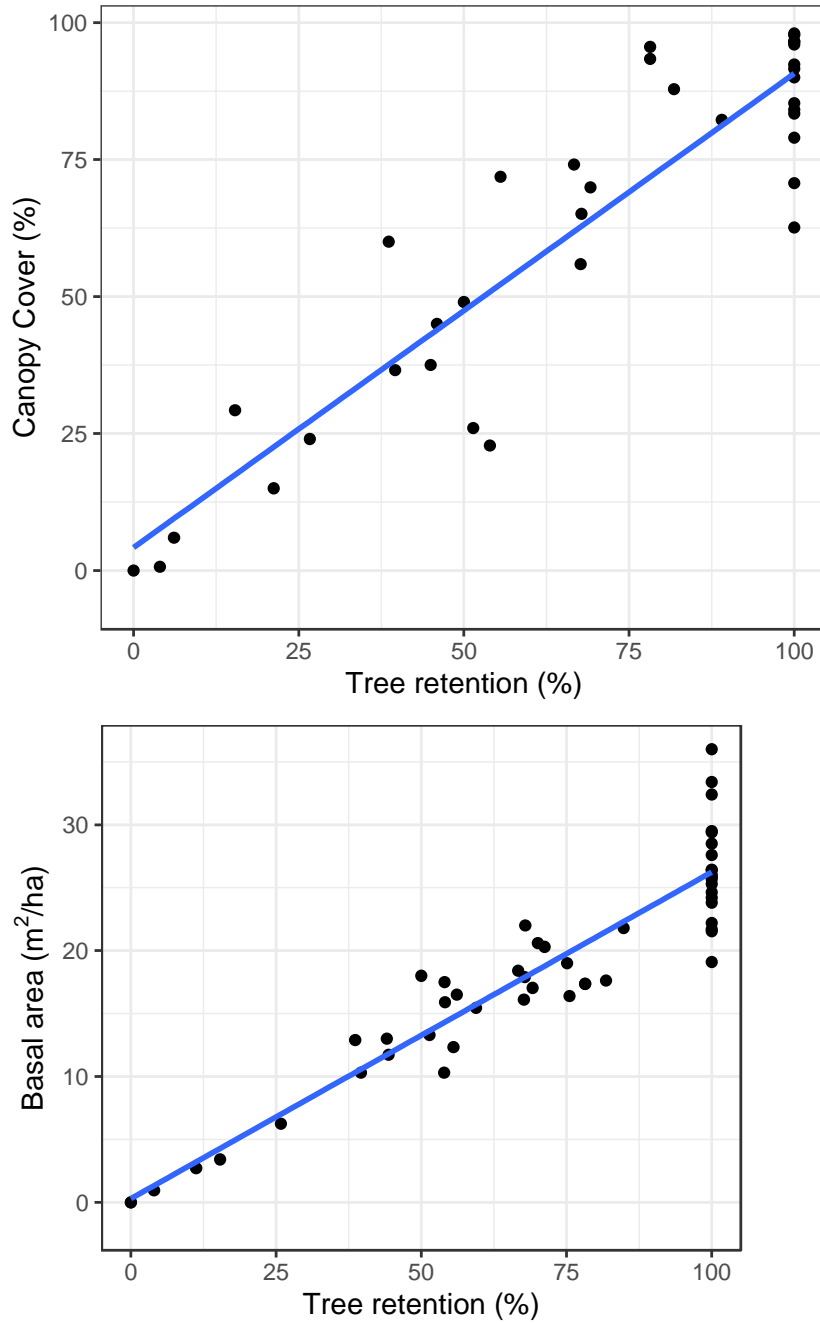
 Fig. A.1. Relationships between percent tree retention and the actual basal area or canopy cover recorded in different treatment levels within a study. All mature forest stands were deemed 100% tree retention, while the tree retention values for harvested stands were based on the proportion of the basal area or canopy cover of the mature forest stand for that given study (see Methods section for more details). Some studies lacked data on basal area (and just had canopy cover), and thus basal area could not be used as a baseline measure (e.g., predictor variable) for comparison among studies.
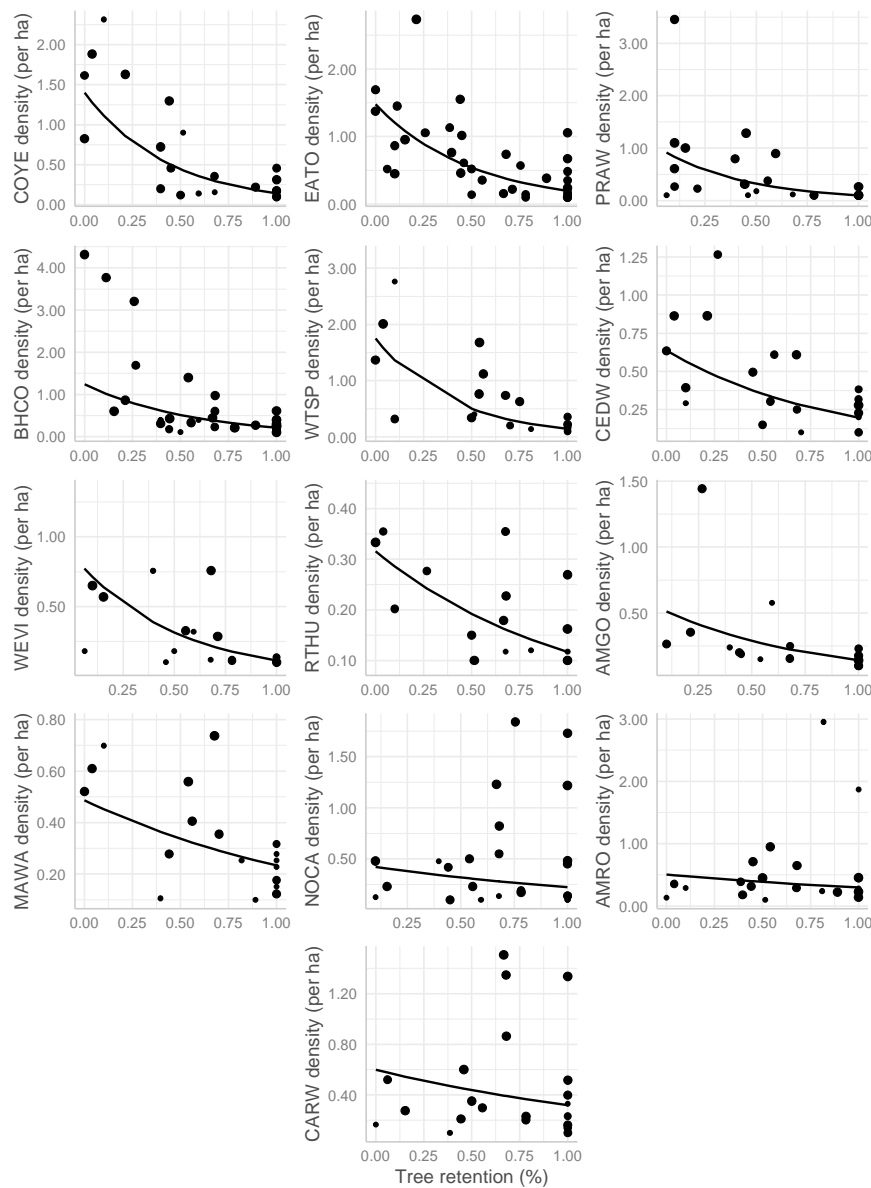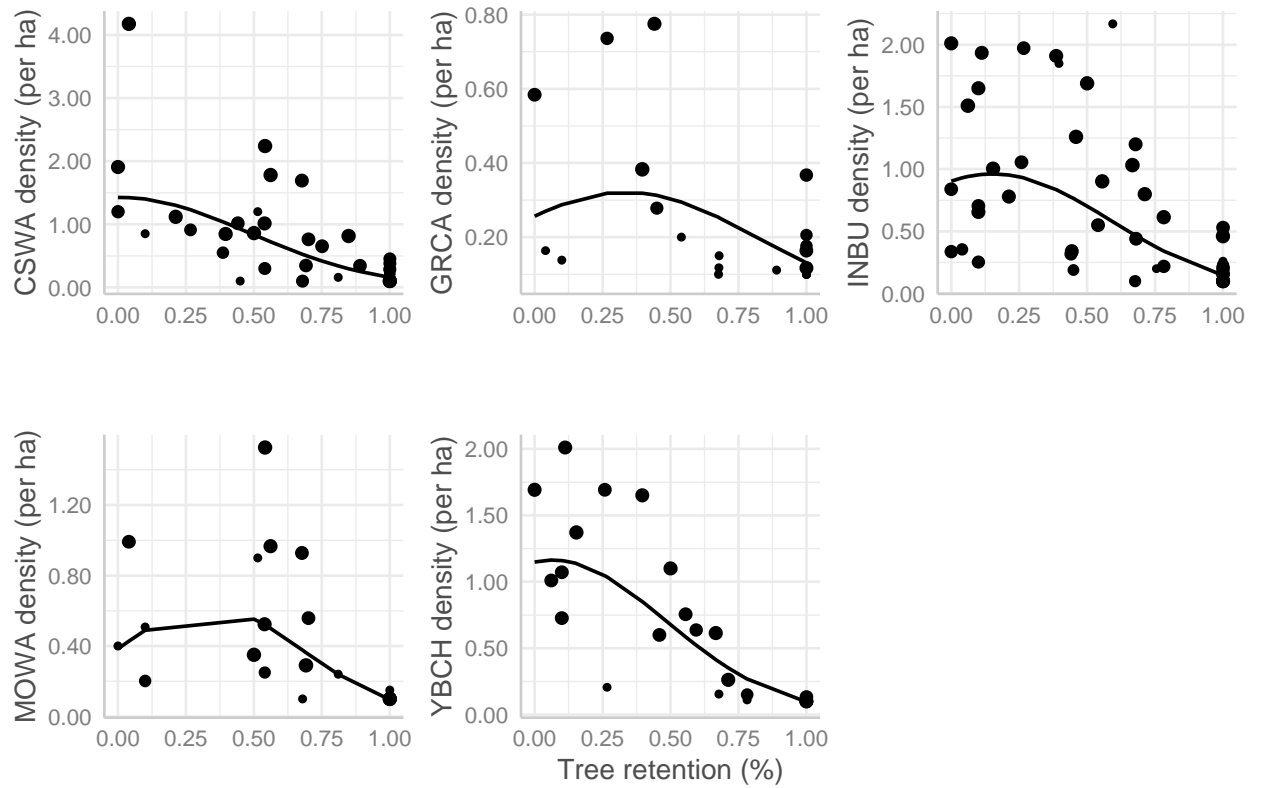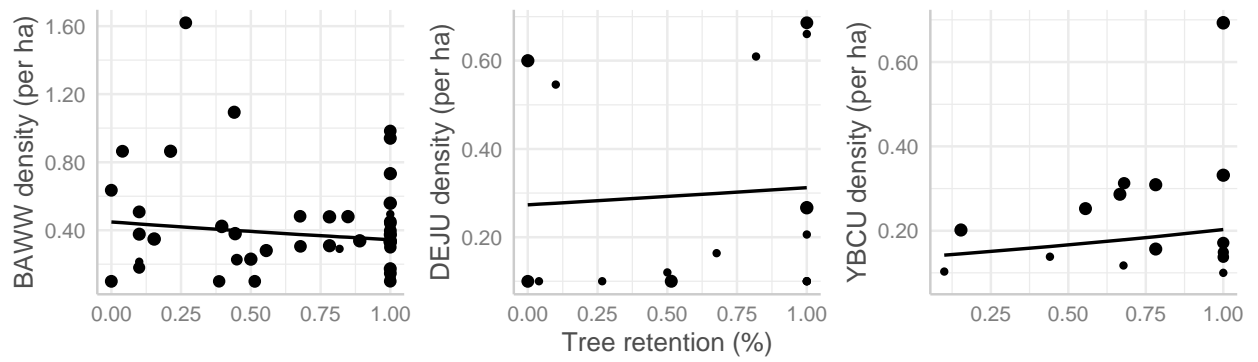
Fig. A.2. Effect of tree retention on avian density in forestry stands across the eastern United States, for shrubland species in which the null model was the best fit. Black-and-white warbler (BAWW) had 43 data points from 19 studies, dark-eyed junco (DEJU) had 16 data points from 7 studies, and yellow-billed cuckoo (YBCU) had 15 data points from 6 studies.

II. **Effects of Forest Management on the Conservation of Bird Communities in Eastern North America: A Meta-analysis**

Summary: Forest management affects conditions for both shrubland and mature-forest birds, and managers require information for balancing the ostensibly opposing habitat needs of both bird guilds. Although numerous studies exist describing the effects of forestry on birds, studies are often limited in scope and typically examine silvicultural treatments within discrete categories, potentially limiting their application to management elsewhere. We synthesized the results of previous studies by conducting a meta-analysis to first examine the effects of tree harvests on mature-forest bird species abundance in eastern North America. We then combined these mature-forest bird results with those from a previous meta-analysis examining tree harvests and shrubland birds, to illustrate how the overall forest-shrubland avian community changes along a gradient of tree retention. We found densities of eighteen mature-forest bird species generally declined as tree retention and basal area decreased, although the strength and shape of this relationship varied among species. A few mature-forest species such as ovenbird (*Seiurus aurocapilla*) and brown creeper (*Certhia americana*) declined in abundance with any amount of tree harvesting. In contrast, several forest bird species, such as wood thrush (*Hylocichla mustelina*) and yellow-bellied sapsucker (*Sphyrapicus varius*), had similar abundances among unharvested and partially harvested (e.g., shelterwood) stands, and others, like least flycatcher (*Empidonax minimus*) and eastern wood-pewee (*Contopus virens*), had their highest abundances in shelterwoods. Because any form of forest management favors some species over others, we weighted standardized, predicted individual species densities by Partners-in-Flight conservation values, and then summed these per-species weighted densities to generate an objective community-wide conservation index. We found that clearcuts and partially harvested stands typically had the highest conservation values, and unharvested and lightly-harvested stands (70-100% tree retention) had the lowest conservation scores. Many declining shrubland bird species of conservation concern are abundant in low retention stands, thus elevating the conservation value of these stands. Additionally, high conservation values of partially harvested stands (40-70% tree retention) are due to the presence of some shrubland birds, as well as abundant mature-forest bird species, which are potentially responding to enhanced understory structure resulting from management. In contrast, unmanaged eastern North American forests are generally characterized by low structural diversity relative to conditions historically present in virgin and old-growth forest, and management can create understory structure needed for avian nesting or foraging. Our results can assist managers in assessing species-specific and community-wide responses to tree retention levels along the entire continuous gradient of canopy treatments.

Introduction

In eastern North America, many studies have examined the effects of forest management on breeding bird abundance (e.g., Jobes et al. 2004, Goodale et al. 2009, Akresh and King 2016). High-intensity tree harvests open up the canopy to allow for the growth of dense understory vegetation, which is preferred by many shrubland bird species (Annand and Thompson 1997, Smetzer et al. 2014). In contrast, unharvested forest or lightly thinned

stands typically provide habitat for bird species that need closed-canopy conditions during the nesting period (Webb et al. 1977, Baker and Lacki 1997).

Although informative, the patterns evident in individual studies are subject to variation associated with study-specific bird communities, forest compositions, tree harvest levels, and geographic locations (e.g., Wang et al. 2006, King et al. 2011, Perry et al. 2018), making it challenging to generalize the effects of forestry on birds in eastern North America. A few studies have examined continuous gradients of tree retention (Sheehan et al. 2014, Smetzer et al. 2014), but most studies assess discrete silvicultural treatments (e.g., King and DeGraaf 2000, Pagen et al. 2000), which restricts the inferences of a given study. Quantitative syntheses of previously collected information can provide generalizable findings about the effects of silvicultural harvests of any intensity on the entire bird community, which can then guide the activities of managers and conservationists (Vanderwel et al. 2007, Schlossberg and King 2015).

Specifically, meta-analyses can effectively summarize findings across individual studies (Arnqvist and Wooster 1995). Previous meta-analyses have been used to better understand the effects of forest management on birds (e.g., Schiek and Song, 2006; Fontaine and Kennedy, 2012; Fedrowitz et al., 2014, LaManna and Martin 2017). For example, Akresh et al. (2021) recently completed a meta-analysis on 21 putative shrubland bird species and presented quantitative relationships between tree retention percentage and bird density.

Meta-analyses can enable synthesized predictions of the bird community response to silvicultural prescriptions; however, balancing the opposing needs of shrubland and mature-forest birds is challenging because both these two species groups merit conservation attention but can occupy opposite ends of the gradient of silvicultural intensity. Mature-forest birds that require tree canopies such as wood thrush (*Hylocichla mustelina*) and cerulean warbler (*Setophaga cerulea*) have exhibited steep range-wide declines over recent decades (King et al. 2006; Buehler et al. 2008; Sauer et al. 2019). Additionally, a high proportion of open-canopy, shrubland bird species such as prairie warbler (*Setophaga discolor*), field sparrow (*Spizella pusilla*), and eastern towhee (*Pipilo erythrophthalmus*) are also declining range-wide (Dettmers, 2003; King and Schlossberg, 2014).

One approach to balancing bird species with contrasting habitat requirements is with the use of community conservation scores (Nuttle et al. 2003). Conservation scores for a community of birds can be calculated by weighing the abundances of different individual species depending on their threatened status and regional population abundance, and then summing across species to calculate a conservation score for the entire forest-shrubland bird community (Götmark et al. 1986, Hunter et al. 1993). Community conservation scores can be more useful to conservationists and managers than solely examining species richness, which does not consider the conservation status of each individual species (Beissinger et al. 2000, Carter et al. 2000, Pons et al. 2003).

Partners-in-Flight (PIF) values from the Avian Conservation Assessment Database (Panjabi et al. 2020) are particularly useful and have been used by previous studies to characterize the conservation status of individual species in eastern North America and to create community-wide conservation values (Nuttle et al. 2003, Paquet et al. 2006). For example, Twedt et al. (2002) calculated conservation values for the entire bird community in three bottomland hardwood forest types in the southern U.S, using

individual-species PIF scores. In a recent paper, Twedt (2020) conducted a meta-analysis on the effects of time since treatment and harvest intensity on community conservation values using primary studies on bird abundance throughout North America. Twedt (2020) found that community-wide conservation scores were highest in hardwoods stands with 30-50% retention and in conifer stands with 50-70% retention, but recommended that regional examinations of bird responses to harvest intensities would be useful given potential variation among regions (Fedrowitz et al. 2014).

In this study, we examined the effect of tree retention percentage on the abundance of individual mature-forest bird species in eastern North America, and then combined these mature-forest bird relationships with our previous data on shrubland birds (Akresh et al. 2021) to calculate community-wide conservation scores along the same gradient of harvest intensity. We conducted the meta-analysis with data from previously published studies, and in our community-wide analyses, we weighed individual species using Partners-in-Flight conservation values. Data were analyzed along a continuous gradient of tree retention, and we also examined bird responses among three discrete silvicultural classifications (clearcuts, shelterwoods, and high-retention stands) that are familiar forestry prescriptions. The results from this categorical analysis can be compared with past studies, and may allow for better planning and communication with forest managers (Lott et al. 2021). We ran community-wide analyses separately for four different North American Bird Conservation Regions (North American Bird Conservation Initiative 2020), focusing on regions in northeastern North America, and tested effects of removing specific species from the calculations. By having data-based estimates of harvest impacts at both the individual species and community level, forest managers can better plan their management activities and understand the tradeoffs of any given harvesting treatment on forest and shrubland birds.

Methods
Mature-forest Birds Meta-analyses
We searched for studies examining mature-forest birds and silviculture in eastern North America, by searching Google Scholar and Web of Science databases with the following search terms: "bird", and/or "avian", and "residual tree", "green tree retention", "shelterwood", "single-tree selection", "thinning", "seed-tree", "clearcut", "regenerating forest", or "timber harvest" (Lott et al. 2019). We also examined reference lists and used 'snowballing' techniques (Wohlin, 2014). We included the studies used in Akresh et al. (2021) that examined mature-forest birds.

The extent of our study was the eastern United States and southeastern Canada, and did not include western North America or the boreal forest. We chose to include community bird studies that presented either bird density estimates or abundance data that could be standardized by unit area. We did not include studies focused on just one individual species because they may have had different survey methods (e.g., mapping color-banded birds) and could have introduced publication bias into our study (Gurevitch and Hedges, 1999).

Species were designated as "mature-forest" birds if they were associated with closed-canopy forest in studies of bird communities across conditions or gradients of silvicultural intensity (e.g., Annand and Thompson 1997, King and DeGraaf 2000). We did not include generalist bird species that occupy forests, but are also present in non-forest habitats such as suburban neighborhoods and urban parks (e.g., downy woodpecker

[*Picoides pubescens*], white breasted nuthatch [*Sitta carolinensis*]; Kluza et al. 2000). We collected data on 26 species: yellow-bellied sapsucker (*Sphyrapicus varius*), least flycatcher (*Empidonax minimus*), great-crested flycatcher (*Myiarchus crinitus*), Acadian flycatcher (*Empidonax virescens*), eastern wood-pewee (*Contopus virens*), red-eyed vireo (*Vireo olivaceus*), blue-headed vireo (*Vireo solitarius*), brown creeper (*Certhia americana*), winter wren (*Troglodytes hiemalis*), golden-crowned kinglet (*Regulus satrapa*), red-breasted nuthatch (*Sitta canadensis*), wood thrush, Swainson's thrush (*Catharus ustulatus*), veery (*Catharus fuscescens*), hermit thrush (*Catharus guttatus*), blue-grey gnatcatcher (*Polioptila caerulea*), American redstart (*Setophaga ruticilla*), pine warbler (*Setophaga pinus*), ovenbird (*Seiurus aurocapilla*), black-throated green warbler (*Setophaga virens*), black-throated blue warbler (*Setophaga caerulescens*), blackburnian warbler (*Setophaga fusca*), yellow-rumped warbler (*Setophaga coronata*), hooded warbler (*Setophaga citrina*), scarlet tanager (*Piranga olivacea*), and rose-breasted grosbeak (*Pheucticus ludovicianus*; Annand and Thompson 1997, King and DeGraaf 2000). However, not all of these species had enough data for analysis (see below).

Studies included a wide range of silvicultural harvests, such as single-tree selection, tree thinning, shelterwood, retention harvest, even-aged reproduction (EAR), seed-tree, and clearcuts. Group selection cuts were included if the harvests were less than 0.5 ha (range = 0.05-0.4 ha), to be certain that openings were interspersed throughout a much larger forested stand. For the few excluded studies with group selection cuts between 0.5 and 1 ha, we were uncertain what was the proportion of bird surveys that were conducted within these larger openings or in the adjacent, unharvested forest. Our study only focused on tree harvests in naturally regenerating forests, and thus we excluded studies examining the effects of fire or other natural disturbances, and studies in tree plantations.

We focused on studies with harvested stands < 16 years since treatment (Schlossberg and King 2009). Studies often averaged bird abundance across multiple stands with different years since treatment (see Table 1 in Akresh et al. 2021), so we did not attempt to examine time since treatment in our analyses. Moreover, some studies did not present year since treatment values for unharvested stands, or this was complicated by historic selective tree harvesting and high-grading within stands (Supplementary Material). Throughout our paper, we are using the terms 'unmanaged' and 'unharvested' forest to classify reference or control forest stands within primary studies that were not recently managed, but we note that almost all eastern North American forests have likely had some tree harvesting in the last 150-200 years (Litvaitis, 1993; Foster et al., 1998) and the forest stands within primary studies we examined were not structurally complex, old-growth or virgin stands found in pre-colonial North America (Keeton 2006). For studies that provided information on the age of unmanaged, reference forest stands, most unmanaged stands had not been previously logged for 50-120 years (Supplementary Material).

We determined the percent tree retention levels of treated stands in each study by taking the ratio of the mean basal area of treated stands versus the control, unmanaged forest stands. We classified unmanaged forest stands as having 100% tree retention. The percent tree retention values were highly correlated with basal area values (Appendix Figure 1, r = 0.93). In studies that did not present basal area, we used percent canopy cover instead to determine the tree retention percentage. Several studies in clearcuts did

not present vegetation data (e.g., McDermott and Wood 2009), but we included these studies because sample sizes for this treatment type were limited. We assigned a 0% retention level for studies that did not mention any residual trees in the clearcut stands, and assigned a 10% tree retention level for studies which mentioned clearcuts contained a small number of residual trees.

We recorded general data from each study (e.g., study location, survey method), as well as the raw mean abundance or density and their standard errors (SEs) for each species in the treated and unharvested stands, and data on basal areas and canopy cover of the stands (Supplementary Material). We used Web Plot Digitizer Version 4.1 (Rohatgi, 2018) to obtain data from figures. We then standardized all avian data to the number of birds/ha (Akresh et al. 2021). For point count studies, we divided the raw mean abundance by the point count circle radius (e.g., 40m, 50m, 75m), to convert the data to a standardized density estimate. For a few studies with unlimited-distance point counts, we used a 75m radius because detection probability declines past 50m (Schieck, 1997; Reidy et al., 2011; Newell et al., 2013). For a given study, we included the species-specific abundance or density only if the species had an abundance > 0 in either treated or unmanaged stands (i.e., the species was present in the study location), because studies were conducted outside of the range limits of at least some of our focal species.

As in Schlossberg and King (2009) and Akresh et al. (2021), we conducted a regression-type meta-analysis using data of mean densities of birds recorded in forest stands with different tree retention levels. We did not use more formal meta-analyses methods (e.g., Hedges et al., 1999; Kalies et al., 2010; Tilghman et al., 2012), because we were often unsure of the true sample size of surveys (Hurlbert, 1984; Spake and Doncaster, 2017) and we wanted to conduct the same standardized analysis as Akresh et al. (2021) to combine both analyses for the community conservation scores. We weighted each bird density data point by dividing the SE by the mean density, and then standardizing this weight to a value ranging between 1 and 2 (Vanderwel et al., 2007). Density data with smaller SEs had higher weights. For density values of 0, we conservatively inputted the lowest real-number weight computed for the other retention level(s) in the same study for that given species (Vanderwel et al., 2007). Several studies did not present standard errors (n = 6); for these data we used a weight of 1 (the lowest weight possible).

We conducted analyses on species with at least 15 data points (i.e., species-specific mean bird densities at different treatment levels within studies), and we ran weighted Generalized Linear Mixed Models (GLMM) separately for each species. We used Gamma distributions with a log link, and added 0.1 to all bird densities in order to use Gamma functions with density data that included 0's (Kalies et al., 2010, Akresh et al. 2021). The tree retention percentage was a continuous predictor variable and bird density was the response variable. We included a random effect of study which accounted for variation among studies and multiple data values for a given species within studies (Fontaine and Kennedy, 2012). We attempted to examine relationships within forest types (e.g., Oak-Hickory versus Northern Hardwoods), but the data was not sufficient within each species to run these models.

We used an information-theoretic approach to compare three models for each species: a null model, a model with a linear predictor of tree retention, and a model with a quadratic and linear predictor of tree retention. We used Akaike's Information Criterion

values corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002) to compare among models. We defined the top model as the model with the lowest AIC$_c$, if the top model was more than 2 AIC$_c$ values compared with the next highest supported model. If there were several models within 2 ΔAIC$_c$ values, we chose the simplest model as our top model (Arnold, 2010). A few mixed models did not converge when conducting model selection (for four species); in these cases, we ran simpler fixed-effects models without the random effect of study.

In addition to testing a continuous predictor of tree retention, in separate models we compared bird densities among discrete, categorical levels of silvicultural treatments. Following Akresh et al. (2021) and based on basal areas and forest type, we assigned treatment levels in each study to either regeneration harvests with low retention, regeneration harvests with moderate retention (e.g., shelterwoods), or high retention (often unmanaged) stands. Separately for each species, we conducted similar weighted GLMMs to examine categorical levels of treatment types. Bird density was still the response variable, and we now included a main categorical predictor variable with three retention levels: low, moderate, and high. The GLMM did not converge for hermit thrush, and we used a simpler, fixed-effect model for this species. All analyses were conducted in the R statistical program version 4.0.3 (R Core Team, 2020), and we used the lme4 and lmerTest packages to conduct mixed-effect models (Bates et al., 2015; Kuznetsova et al., 2016), and the ggeffects package for plotting predictions (Lüdecke, 2018).

Community-wide Analyses
In order to determine the impact of silvicultural intensity on the entire forest-shrubland bird community, we also examined the relationship between percent forest retained and a community-wide conservation index incorporating both shrubland and forest birds. We first selected the top model (a null, linear, or quadratic relationship with tree retention), for each shrubland and mature-forest species, using shrubland bird relationships from a previous study (Akresh et al. 2021). Shrubland bird species consisted of American goldfinch (*Spinus tristis*), brown-headed cowbird (*Molothrus ater*), cedar waxwing (*Bombycilla cedrorum*), common yellowthroat (*Geothlypis trichas*), eastern towhee, magnolia warbler (*Setophaga magnolia*), northern cardinal (*Cardinalis cardinalis*) , prairie warbler, ruby-throated hummingbird (*Archilochus colubris*), white-eyed vireo (*Vireo griseus*), white-throated sparrow (*Zonotrichia albicollis*), chestnut-sided warbler (*Setophaga pensylvanica*), gray catbird (*Dumetella carolinensis*), indigo bunting (*Passerina cyanea*), mourning warbler (*Geothlypis philadelphia*) and yellow-breasted chat (*Icteria virens*). With the top mixed model fit for each species, we then predicted the mean density of each species as forest retention increased at 1% increments between 0-100%. We then standardized the predicted density values per species to values between 0-1, because we wanted to compare the impact of tree retention on individual species, regardless of variation in density due to geographic, study, or site-level factors that were unrelated to tree retention. Several shrubland birds also had relatively high recorded densities (> 1 bird per ha; Akresh et al. 2021) compared to mature-forest birds, but we were unsure if this was due to increased detectability of females of shrubland birds in clearcuts or other survey-related biases (Pagen et al. 2002). Therefore, our meta-analysis approach differed from previous studies (e.g., Twedt et al. 2002, Twedt 2020) in that we created community-wide indexes that were not location-specific, but rather were based on

standardized abundance across the tree retention gradient and were only using selected species that had enough data to determine quantitative relationships with tree retention.

We obtained region-specific values of per-species conservation scores based on Partners in Flight criteria (Carter et al. 2000). Specifically, from the Partners in Flight database, we obtained Regional Concern Scores (breeding season; RCS-b) for each species, for each of the following Bird Conservation Regions (BCR): 13, 14, 28, and 30 (North American Bird Conservation Initiative 2020). The RCS-b conservation score is a combination of scores from individual elements of conservation status, such as global population size, breeding distribution, population trend, threats to breeding populations, and regional density, all of which are ranked on a scale of 1 to 5 (Panjabi et al. 2020). We focused on BCR regions in the northeastern U.S and southeastern Canada; we did not include BCR 29, a more southern region that did not have PIF scores for seven focal species, or other BCRs that lacked some of our focal species.

Across the gradient of forest retention (0-100%), we multiplied the standardized predicted density values from our models with the regionally specific PIF conservation scores, for each given species (Nuttle et al. 2003). This effectively integrated and weighted the species relative density values with their conservation values. Lastly, we computed a community-wide conservation score for each percentage of forest retention by summing the per-species values across both forest and shrubland species (Nuttle et al. 2003). We computed the community-wide conservation scores separately for each BCR. We were primarily interested in the mean relationships between community conservation scores and tree retention, and did not incorporate study-specific or species-specific variation around the mean predicted values.

We chose to include an equal number of shrubland and mature-forest bird species when computing our community-wide conservation scores, in order to effectively examine a balance of sustaining and conserving both mature-forest and shrubland bird populations. We did not include species in which the null model was the top model, or species in which the effect of forest retention on bird density was not significant (using an alpha level of 0.05). These species were not greatly influenced by tree retention and would only add a constant value to our community-wide conservation index, but would not change the relationship of the index with forest retention. Given that there were a few more shrubland species compared to mature-forest species which we observed a significant effect of tree retention, we discarded two shrubland bird species (Carolina wren [*Thryothorus ludovicianus*] and American robin [*Turdus migratorius*]) in our community-wide conservation scores; these two species had weak relationships with tree retention (Akresh et al. 2021) and are weakly associated with shrublands (Schlossberg and King 2007). Afterwards, our community-wide conservation scores in BCRs 13, 28, and 30 combined values from 16 mature-forest species and 16 shrubland species, all 32 of which had a stronger relationship with tree retention, and had >14 data points to effectively analyze and predict relative abundance in our meta-analysis. BCR 14 is a more northern region and is mostly outside of the range of the yellow-breasted chat (shrubland species) and blue-grey gnatcatcher (mature-forest species; Sullivan et al. 2009). Thus, we excluded these two species in our community-wide conservation scores for BCR 14.

Overall, we note that although our community-wide conservation scores were tallied from a representative group of species found in the forests of northeastern North

America, the community-wide conservation scores are specific to the species that we were able to include in our analyses. Given this, we tested how much the community-wide conservation scores changed if certain species were taken out of the calculations. Separately for each region, we conducted a 'delete-one' jackknife analysis (Crowley 1992, Princé and Zuckerberg 2015), in which we iteratively deleted one species from the calculations of the community-wide conservation scores for every predicted value of forest retention between 0-100%. We then used the 0.025, 0.50, and 0.975 quantiles of the jackknifed conservation scores to examine the variation in the relationship between forest retention and the community-wide conservation scores when deleting individual species from our original candidate set of species.

Finally, we calculated community conservation scores among discrete categories of silvicultural intensities: low, moderate, and high tree retention. Within categories, we used the mean basal area from treatments within studies; 5.6 m^2/ ha for low retention, 15.7 m^2/ha for moderate retention, and 24.7 m^2/ ha for high retention (Akresh et al. 2021). We then converted these basal area values to percent tree retention levels (27%, 61%, and 91% retention, respectively) using a predicted linear relationship between basal area and tree retention (Appendix Figure 1). Lastly, we presented the 0.025, 0.50, and 0.975 quantiles of the jackknifed conservation scores at these three tree retention levels to examine community-wide conservation scores in representative silvicultural categories.

Results

Mature-forest Bird Relationships

We used data from 33 studies across eastern North America (Figure 1) and acquired adequate data (> 14 density estimates) to fit models for 22 putative mature-forest bird species (Supplementary Material). Based on AIC_c values, most species had support for models with either a linear, or linear and quadratic, continuous predictor of tree retention on bird densities (Table 1). The null model was the top simplest model for five putative mature-forest species: American redstart, great-created flycatcher, hooded warbler, veery, and yellow-rumped warbler. Additionally, although the top model for rose-breasted grosbeak had the linear predictor of tree retention, the effect was not significant (based on the $β_1$, SE, and the p-value; Table 2). Thus, there was little support for a relationship between bird density and a continuous variable of tree retention for these six species (Appendix Figure 2).

Besides rose-breasted grosbeak, seven species had models that fit better with a single linear predictor of tree retention, based on the AIC_c values (Table 2, Figure 2). Predicted bird densities increased as a higher percentage of trees were retained for these seven species: ovenbird, Acadian flycatcher, hermit thrush, black-throated green warbler, brown creeper, red-breasted nuthatch, and wood thrush.

Nine species had models that fit better with quadratic relationships: blue-grey gnatcatcher, blue-headed vireo, blackburnian warbler, black-throated blue warbler, eastern wood-pewee, least flycatcher, red-eyed vireo, scarlet tanager, and yellow-bellied sapsucker. These nine species had more complex relationships with the continuous variable of tree retention (Table 3, Figure 3), but all of these species had lower densities in stands with low tree retention.

Examining densities among three categorical levels of tree retention (Table 4), Acadian flycatcher, blackburnian warbler, brown creeper, black-throated blue warbler, black-throated green warbler, ovenbird, and red-eyed vireo had greatest densities in high

retention stands, had lower densities in shelterwoods (moderate retention) compared to high retention stands, and lowest densities in low retention clearcuts. Eleven other species had more complicated differences in densities among discrete treatment levels (Table 4); although least flycatcher, yellow-rumped warbler, American redstart, eastern wood-pewee, rose-breasted grosbeak, and blue-headed vireo had their highest densities in shelterwoods (moderate tree retention). Wood thrush and yellow-bellied sapsucker had relatively similar densities in high retention stands and shelterwoods, but had lower densities in low retention stands. Blue-grey gnatcatcher, great-crested flycatcher, hooded warbler, and veery densities did not differ among the categorical treatment levels.

Community-wide Conservation Scores
We found non-linear relationships between the community-wide conservation scores and tree retention in four Bird Conservation Regions (Figure 1, 4), which we examined by combining an equal number of mature-forest and shrubland bird species in the community-wide scores (Table 5). The community-wide scores generally had two peaks: in stands with very low tree retention (0-10%) and in stands with moderate tree retention (40-70%). The relative importance (or amplitude) of the two peaks varied among BCRs (e.g., in BCR 30, the 40-70% peak was relatively lower than the peak at 0-10% tree retention, while BCR 14 showed the opposite in peak amplitude). The relationship in BCR 14 was the most different from the other regions; we did not include two species in the BCR 14 community-wide scores that were included in the other regions. In three of four regions, forest stands with 70-100% tree retention had the lowest community-wide conservation scores, and stands with 85-100% tree retention had the lowest community-wide conservation scores in BCR 14.

To examine the effect of individual species on community-wide scores, we conducted a jackknife analysis and obtained confidence intervals by removing individual species from the community-wide calculations. Examining the area within the confidence intervals in BCRs 13, 28, and 30, the effect of tree retention on the community-wide scores was relatively constant between 0-70% tree retention (Figure 5). In BCR 14, there was a noticeable peak between 40-80% tree retention within the area of the confidence interval. Regardless of the individual species that were removed from the community conservation scores, 85-100% tree retention had the lowest conservation scores across all regions. Examining categorical classifications of silvicultural intensities, community conservation scores were highest in shelterwoods and low retention stands, and lowest in high-retention and unmanaged stands (Table 4).

Discussion
Our findings demonstrate the effects of tree retention and basal area on individual eastern mature-forest bird species, as well as on the entire shrubland-forest avian community in eastern North America. Most putative mature-forest species had their lowest abundance in stands of 0-40% tree retention, as expected from individual studies that demonstrated lower numbers in stands with high levels of canopy removal (e.g., Annand and Thompson 1997, King and DeGraaf 2000), and consistent with the results from a similar meta-analysis of forestry effects on birds by Vanderwel et al. (2007). Low densities of mature-forest species in low-retention stands, which included clearcuts and seed-tree harvests, likely reflect the scarcity of certain habitat elements (e.g., large-diameter trees

and snags, deep leaf litter) needed for these avian species' nesting and foraging requirements (Poulin et al. 2008, Porneluzi et al. 2020).

We found mature-forest species also differed in their responses to canopy removal. Some species (such as the ovenbird and brown creeper) had lower abundance in mid-intensity harvested stands relative to unharvested forests, but the majority of the species had relatively higher or equal abundance in 40-70% tree retention compared to unharvested stands. Individual studies have also documented several mature-forest bird species had high abundance after mid-intensity harvests, such as red-eyed vireos in Missouri (Annand and Thompson 1997), eastern wood peewees in Arkansas (Perry et al. 2018), cerulean warblers in the central Appalachians (Sheehan et al. 2014), and black-throated blue warblers in New Hampshire (King and DeGraaf 2000). These species may have ecological preferences that align with canopy gaps and increased understory vegetation density found in stands with 40-70% tree retention; for instance, black-throated blue warblers prefer dense understory vegetation for nesting (Holway 1991). In contrast, species such as ovenbirds and brown creepers promptly decline in abundance in response to light- to mid-intensity harvests, as found in other studies (Holmes et al. 2004, Tozer et al. 2010, Holmes et al. 2012).

We observed six putative mature-forest species (American redstart, great-crested flycatcher, hooded warbler, veery, yellow-rumped warbler, rose-breasted grosbeak) that were not influenced by the continuous variable of tree retention. Some of these species appear to have broad ecological requirements with respect to canopy closure, and are more influenced by other forest characteristics besides percent tree retention and basal area, such as the density of shrubs, saplings or midstory trees (Hunt 1996, Sheehan et al. 2014, Sherry et al. 2020, Wyatt and Francis 2020). Additionally, for some species, the effect of study explained a large percentage of the variation in our meta-analysis models, which suggests that mature-forest species abundance is also related to other site- and study-specific factors that we did not examine in our analyses. Potentially influential site-specific factors include the characteristics of the reference unmanaged stands, some of which may have had more complex vegetation structure due to past natural or anthropogenic disturbance (Nyland 1992, Faccio 2003, Kelty and D'Amato 2006). Past disturbance at sites could have muddled potential differences between reference and treated forest stands in some studies.

Our findings of mature-forest bird densities among discrete silvicultural categories were similar to our results using a continuous variable of tree retention in the models, although there were some differences between the two analytical approaches. Species like black-throated green warbler and Acadian flycatcher exhibited negative relationships with the continuous variable of tree retention and also had the highest densities in unmanaged and lightly-treated stands. Additionally, species such as yellow-bellied sapsucker and eastern wood-pewee were best fit with a quadratic relationship with tree retention, and had equal or higher densities in shelterwoods compared to high retention stands. In contrast, red-eyed vireo and black-throated blue warbler had their highest densities in high retention stands, then shelterwoods, then low retention stands, but were still best fit with a quadratic relationship. Varied results between the categorical versus continuous tree retention models were likely due to the basal area classifications of shelterwoods we used in our categorical variable (Akresh et al. 2021). As well, small sample sizes within treatments for some species may have influenced the categorical

model results (e.g., < 3 samples of densities for blackburnian warbler, brown creeper, hermit thrush, least flycatcher, red-breasted nuthatch, yellow-bellied sapsucker, and yellow-rumped warbler in low retention stands).

Our community-wide analyses incorporated both individual mature-forest birds as well as shrubland birds, and community-wide conservation scores were highest in stands with 0-70% tree retention in most regions. Specifically, conservation scores had a peak in low retention stands (0-10%) across all BCRs, likely because shrubland bird abundance was high in low retention stands (Akresh et al. 2021) and many shrubland bird species had high per-species PIF scores (Dettmers 2003). Suitable habitat for shrubland birds is geographically restricted (e.g., 6% of northeastern forests), and continues to decline across the eastern United States (King and Schlossberg 2014). As a result, shrubland birds have relatively small, declining populations and are considered important targets for conservation (Litvaitis et al. 1999, Askins 2001), as classified in their PIF conservation scores (Carter et al. 2000). In contrast, mature-forest, unmanaged habitat is far more extensive across most of eastern North America, with the exception of some regions (Brooks 2003, Hanberry and Thompson 2019). Although a few mature-forest avian species are imperiled (King et al. 2006, Rushing et al. 2016), their overall population sizes are greater and population declines less pronounced (Dettmers 2003, Sauer et al. 2019), resulting in lower community conservation scores on average in unharvested stands (King and Schlossberg 2014).

The second peak of high community conservation scores between 40-70% tree retention was perhaps due to the many mature-forest species, and some shrubland species (Akresh et al. 2021), which had quadratic relationships of abundance with tree retention. Species richness has previously been reported to be highest in partially harvested stands due to both the presence of mature-forest species that are able to tolerate or benefit from some reduction in basal area, and shrubland bird species that are generalized enough to tolerate the retained tree canopy (King and DeGraaf 2000). Our analyses go beyond species richness to show partially harvested stands boost community-level conservation values as well. Our results are similar to the findings of Twedt (2020), whose meta-analysis examined studies across North America and observed conservation scores were highest in partially harvested stands of 30-70% tree retention. Interestingly, Twedt (2020)'s analyses differed from our study by using absolute abundances and all species observed at individual study locations to calculate community-wide conservation scores, yet results were mostly consistent in our two different analytical approaches and geographic extents.

We found minimally harvested and unharvested forest stands (70-100% tree retention) had the lowest community conservation scores across most of the BCR regions. These stands do not provide habitat for shrubland birds of conservation concern (Akresh et al. 2021), and we found in our meta-analysis that even some mature-forest species do not reach their peak abundance in unharvested forests in eastern North America. Most forested stands in this region are young relative to the typical lifespan of their constituent tree species (Shifley et al. 2014). Furthermore, many forest stands in eastern North America are even-aged, either having regenerated on cleared agricultural land or after historical clear-cut harvesting (Moola and Vaseur 2008, Shifley et al. 2014), and thus are structurally homogeneous relative to the pre-colonial forests that would have contained large tree fall gaps and multiple age-classes (Keeton 2006). As a result, unmanaged

stands within the study sites we examined in our meta-analyses may have exhibited the relatively depauperate conditions typical of "pole stands," without the self-thinning process from natural tree mortality which creates canopy gaps (Runkle 1981, Moore and Vankat 1986). The lack of canopy gaps and patches of dense understory vegetation in unharvested stands may have led to absences of nesting and foraging sites for shrub- or mid-story avian nesting species (Rankin and Perlut 2015, Schlossberg et al. 2018). Although biologically mature old-growth forest may have higher species richness and conservation value for birds, these stands only represent a tiny fraction of eastern forests (Keeton 2006), and as apparent from the studies we reviewed, are not typically subject to forest management.

Our community-wide findings are generally consistent with smaller scale, primary studies examining conservation scores in the eastern United States, which have also noted higher community conservation scores in managed and restored forests compared to closed-canopy forest stands (Wood et al. 2004, Becker et al. 2011, Singleton et al. 2012, Iglay et al. 2018; although see Norris et al. 2009). Our community-wide results are also consistent with a study in Europe which found that open habitat such as clearcuts had higher conservation scores compared to closed-canopy forests and tree plantations (Paquet et al. 2006). To our knowledge, relatively few studies outside of North America have examined community-wide conservation scores in relation to silviculture, and more research is needed worldwide.

Our examination of community-wide conservation scores was limited by shrubland and mature-forest bird species in which we could obtain enough data points to test a relationship between tree retention and density. When we deleted individual species from the calculations of the community-wide conservation scores in our jackknife analysis, there was more ambiguity in which tree retention percentages produced the highest conservation scores between 0-70% retention. Results between 0-70% tree retention were also slightly different in BCR 14, in which we removed two additional species from the analyses. We therefore caution against suggesting that specific tree retention values between 0-70% would be better to conserve the forest-shrubland bird community as a whole. We do note, however, that unharvested stands had the lowest community-wide conservation scores, and this finding was robust even after removing individual species from the analyses. Although we did not include rarer species in our analyses and community scores, most rare passerine species of conservation concern in eastern North American forests reside in open-canopy, early-successional habitats, such as the golden-winged warbler and Kirtland's warbler (Donner et al. 2010, McNeil et al. 2020), or are abundant in partially harvested stands, such as cerulean warblers (Sheehan et al. 2014). Therefore, inclusion of rare species in our community conservation index may have increased conservation values in harvested stands.

Our study focused only on abundance during the nesting period, although both mature-forest and shrubland birds use early successional, harvested stands extensively during the post-fledging period (Akresh et al. 2009, Chandler et al. 2012, Labbe and King 2014). Additional synthesis and more studies are needed in order to incorporate the post-fledging period (Cox et al. 2014). Nonetheless, given that most forest-nesting bird species use intensively harvested stands for rearing their young and preparing for migration (Marshall et al. 2003, Chandler et al. 2012), the availability of these habitats benefit individuals and populations (Vitz and Rodewald 2006, Stoleson 2013, Cox et al. 2014),

and we did not incorporate the post-fledging period in our meta-analyses, our community-wide conservation scores in open-canopy stands may be conservative.

We did not examine time since treatment in our analyses, and interactions between tree retention and stand age could have influenced our results for individual mature-forest birds and the community conservation values. Some mature-forest birds, such as red-eyed vireos, can increase in abundance as low-retention stands age from 0-15 years since treatment (Perry et al. 2018). In contrast, shrubland bird species often monotonically decline as treated stands age, or have a unimodal response during the first 0-20 years since management (Keller et al. 2003, Schlossberg and King 2009, Akresh et al. 2015). Further research and long-term studies on the interactions between basal area and time since treatment across both shrubland and mature-forest bird communities would be useful for better understanding management effects (Lott et al. 2021).

Conclusion

Our results indicate that in typical, widespread second-growth forest stands in eastern North America, a moderate level of tree harvesting is beneficial for most songbird species, and overall, will increase the avian conservation value of the forest stands. Moderate tree harvesting (e.g., first-entry shelterwood harvests) can increase understory density, which can then increase foraging and nesting opportunities for mature-forest avian species and allow stands to be used by shrubland birds. More intensive timber management (i.e., clearcutting, seed-tree harvests, or second-entry shelterwood harvests) also supports a bird community of high conservation value, by providing open-canopy, dense understory habitat for shrubland birds, which are of high conservation priority regionally.

Although our results will help managers understand the tradeoffs between habitat enhancement for mature-forest and shrubland bird species, they should not be construed as a blanket recommendation to engage in more intensive forestry. Other taxa should also be considered, such as terrestrial salamanders and other amphibians which can decline after timber harvests (Semlitsch et al. 2009, Tilghman et al. 2012), as well as other site, landscape, and region-specific considerations (Aust and Blinn 2004, Betts et al. 2007, Bradford and D'Amato 2012). Some forests, especially biologically mature stands >150 years old, will already have developed important structural characteristics that can enhance habitat conditions for mature-forest birds, without forest management needed (Haney 1999, Kirk et al. 2012). Rather than promoting more intensive forestry across eastern North America, it is our hope that our results will help managers to achieve a balance among forest conditions needed to maintain populations of all native bird species and other wildlife that a given site or landscape can potentially support.

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Table 1. Model comparisons of a null, linear, or quadratic relationship between percent tree retention and bird density for each putative mature-forest species. We compared models using values of Akaike's Information Criterion corrected for small sample sizes (AIC_c). For each species, we defined the top model as the model with the lowest AIC_c value, if the difference in AIC_c from the top model to the next highest supported model (ΔAIC_c) was >2. If multiple models were had <2 ΔAIC_c, indicating similar support, we defined the simplest model of these (i.e., Null or Linear) as the top model.

Species	ΔAIC_c Null	ΔAIC_c Linear	ΔAIC_c Quad	Top simplest model
American redstart	0	1.691	4.198	Null
Great-crested flycatcher	0	2.522	1.587	Null
Hooded warbler	0	2.362	5.224	Null
Veery	0	2.422	5.219	Null
Yellow-rumped warbler	0.736	4.152	0	Null
Acadian flycatcher	82.1	1.582	0	Linear
Brown creeper	8.505	0	4.363	Linear
Black-throated green warbler	51.751	0	0.988	Linear
Hermit thrush	18.982	0	2.378	Linear
Ovenbird	67.938	0	1.79	Linear
Rose-breasted grosbeak	2.123	0	2.438	Linear
Red-breasted nuthatch	2.799	0	4.231	Linear
Wood thrush	3.875	0	2.706	Linear
Blue-grey gnatcatcher	2.588	3.896	0	Quadratic
Blue-headed vireo	14.325	13.745	0	Quadratic
Blackburnian warbler	17.183	4.429	0	Quadratic
Black-throated blue warbler	22.095	5.814	0	Quadratic
Eastern wood-pewee	26.658	28.877	0	Quadratic
Least flycatcher	16.904	20.072	0	Quadratic
Red-eyed vireo	77.305	12.725	0	Quadratic
Scarlet tanager	13.963	2.72	0	Quadratic
Yellow-bellied sapsucker	29.932	23.219	0	Quadratic

Table 2. For mature-forest bird species in which the top model included the linear predictor of tree retention, we present the number of data points (n; i.e., mean bird densities in different treatment levels within studies), the number of studies which had data for the given species, percent of the model variance accounted for by the random effect of study, model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate) and their SEs in parentheses, t values, and p-values. The percent of the variance accounted for by the random effect of study was computed by dividing the variance of the random effect with the total variance in the model (the variance of the random effect plus the residual variance; Zuur et al. 2009). The mixed effects model did not converge for rose-breasted grosbeak, and we used a fixed effects model for this species. Species are listed in order of the strength of the model, based on the t value.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	t	p
Ovenbird	62	26	0.648	-2.284 (0.218)	2.313 (0.121)	19.2	<0.001
Acadian flycatcher	30	13	0.789	-2.113 (0.265)	1.124 (0.072)	15.6	<0.001
Hermit thrush	22	10	0.593	-2.315 (0.267)	1.681 (0.161)	10.5	<0.001
Black-throated green warbler	33	15	0.619	-1.860 (0.248)	1.509 (0.145)	10.4	<0.001
Brown creeper	16	7	0.169	-2.328 (0.236)	1.154 (0.275)	4.2	<0.001
Red-breasted nuthatch	15	7	0.774	-1.915 (0.282)	0.290 (0.101)	2.9	0.004
Wood thrush	36	15	0.495	-1.667 (0.195)	0.361 (0.140)	2.6	0.01
Rose-breasted grosbeak	31	14	NA	-0.514 (0.453)	-0.711 (0.589)	-1.2	0.24

Table 3. The number of data points (n), the number of studies included, the proportion of variance accounted for by the random effect of study, and model parameter estimates (β_0 = intercept, β_1 = linear parameter estimate, β_2 = quadratic parameter estimate) and their SEs in parentheses for mature-forest bird species, in which the top model included a linear and quadratic predictor of tree retention.

Species	n	No. studies	% variance	β_0 (SE)	β_1 (SE)	β_2 (SE)
Blue-grey gnatcatcher	28	11	0.648	-1.476 (0.302)	1.964 (0.646)	-1.492 (0.534)
Blue-headed vireo	20	9	0.482	-3.370 (0.387)	7.507 (1.205)	-5.653 (1.034)
Blackburnian warbler	15	7	0.640	-3.123 (0.370)	4.647 (0.899)	-2.650 (0.740)
Black-throated blue warbler	28	12	0.485	-2.123 (0.283)	3.743 (0.872)	-2.215 (0.711)
Eastern wood-pewee	59	24	0.513	-1.948 (0.191)	3.217 (0.520)	-2.564 (0.414)
Least flycatcher	17	7	0.429	-2.978 (0.374)	7.835 (0.946)	-5.387 (0.724)
Red-eyed vireo	64	27	0.646	-1.464 (0.212)	2.877 (0.444)	-1.483 (0.363)
Scarlet tanager	49	21	0.566	-1.899 (0.220)	1.962 (0.636)	-1.200 (0.513)
Yellow-bellied sapsucker	19	9	0.844	-2.196 (0.428)	4.081 (0.471)	-2.689 (0.373)

Table 4. Mature-forest bird density and community-wide conservation scores among categorical silvicultural treatments in the eastern United States. Presented are model-predicted mean density estimates per bird species and per category, with 95% confidence intervals in parentheses. Low-retention harvests include any stands with basal areas less than shelterwoods, while high-retention includes any stands with basal areas greater than shelterwoods (see Table 2 in Akresh et al. (2021) for basal area classifications by forest type). For individual bird species, '>' classifies statistically significant ($p < 0.05$) differences in bird density between treatment types, while '=' denotes non-significance. Estimates with shared letter superscripts are not statistically different. For community conservation scores, presented are the median and 95% confidence intervals of the jackknife analysis at 27%, 61%, and 91% tree retention (5.6, 15.7, and 24.7 m^2/ha, respectively).

Species	Low retention harvests	Moderate retention (shelterwood)	High retention stands
High retention > shelterwood > low retention			
Acadian flycatcher	0.15^a (0.09-0.25)	0.27^b (0.16-0.46)	0.35^c (0.21-0.58)
Blackburnian warbler	0.05^a (0.03-0.10)	0.25^b (0.13-0.47)	0.32^c (0.17-0.61)
Brown creeper	0.10^a (0.05-0.17)	0.18^b (0.12-0.27)	0.30^c (0.22-0.40)
Black-throated blue warbler	0.15^a (0.09-0.28)	0.41^b (0.26-0.63)	0.57^c (0.38-0.86)
Black-throated green warbler	0.17^a (0.10-0.30)	0.38^b (0.23-0.64)	0.69^c (0.43-1.12)
Ovenbird	0.15^a (0.10-0.24)	0.41^b (0.27-0.63)	0.95^c (0.64-1.41)
Red-eyed vireo	0.36^a (0.24-0.53)	0.76^b (0.52-1.11)	0.92^c (0.64-1.31)
High retention > shelterwood = low retention			
Scarlet tanager	0.24^a (0.17-0.35)	0.25^a (0.17-0.36)	0.32^b (0.23-0.45)
High retention > low retention, high retention = shelterwood, shelterwood = low retention			
Red-breasted nuthatch	0.14^a (0.08-0.26)	0.18^{ab} (0.11-0.31)	0.19^b (0.11-0.33)
High retention = shelterwood > low retention			
Hermit thrush	0.10^a (0.04-0.29)	0.39^b (0.22-0.68)	0.58^b (0.36-0.91)
Wood thrush	0.18^a (0.13-0.27)	0.28^b (0.19-0.40)	0.26^b (0.19-0.37)
Yellow-bellied sapsucker	0.14^a (0.06-0.32)	0.49^b (0.22-1.13)	0.46^b (0.20-1.04)
Shelterwood > high retention > low retention			

Least flycatcher	0.05[a] (0.03-0.10)	0.90[c] (0.58-1.39)	0.62[b] (0.42-0.93)
Yellow-rumped warbler	0.18[a] (0.10-0.32)	0.36[c] (0.22-0.58)	0.28[b] (0.17-0.44)
Shelterwood > high retention = low retention			
American redstart	0.30[a] (0.18-0.49)	0.53[b] (0.35-0.82)	0.38[a] (0.26-0.55)
Eastern wood-pewee	0.24[a] (0.17-0.32)	0.41[b] (0.31-0.54)	0.28[a] (0.21-0.36)
Shelterwood > high retention, shelterwood = low retention, high retention = low retention			
Rose-breasted grosbeak	0.30[ab] (0.17-0.54)	0.36[b] (0.22-0.60)	0.24[a] (0.15-0.39)
Shelterwood > low retention, shelterwood = high retention, high retention = low retention			
Blue-headed vireo	0.12[a] (0.06-0.28)	0.39[b] (0.20-0.76)	0.24[ab] (0.14-0.41)
High retention = shelterwood = low retention			
Blue-grey gnatcatcher	0.38[a] (0.22-0.63)	0.39[a] (0.22-0.69)	0.37[a] (0.23-0.60)
Great-crested flycatcher	0.19[a] (0.13-0.27)	0.23[a] (0.17-0.30)	0.18[a] (0.15-0.23)
Hooded warbler	0.31[a] (0.17-0.56)	0.24[a] (0.12-0.46)	0.27[a] (0.18-0.42)
Veery	0.42[a] (0.24-0.75)	0.40[a] (0.25-0.63)	0.35[a] (0.23-0.55)
Community-wide conservation scores			
BCR 13	205 (199-210)	209 (201-213)	189 (182-194)
BCR 14	211 (204-215)	223 (215-227)	206 (199-212)
BCR 28	232 (227-238)	236 (228-240)	215 (206-219)
BCR 30	225 (219-229)	228 (220-232)	211 (201-216)

Table 5. Mature-forest and shrubland species (Akresh et al. 2021) included in the community-wide conservation scores and their relationships with tree retention.

Species	Guild / overall relationship with tree retention	Best model with tree retention
Acadian flycatcher	Forest / Positive	Linear
Brown creeper	Forest / Positive	Linear
Black-throated green warbler	Forest / Positive	Linear
Hermit thrush	Forest / Positive	Linear
Ovenbird	Forest / Positive	Linear
Red-breasted nuthatch	Forest / Positive	Linear
Wood thrush	Forest / Positive	Linear
Blue-grey gnatcatcher	Forest / Positive	Quadratic
Blue-headed vireo	Forest / Positive	Quadratic
Blackburnian warbler	Forest / Positive	Quadratic
Black-throated blue warbler	Forest / Positive	Quadratic
Eastern wood-pewee	Forest / Positive	Quadratic
Least flycatcher	Forest / Positive	Quadratic
Red-eyed vireo	Forest / Positive	Quadratic
Scarlet tanager	Forest / Positive	Quadratic
Yellow-bellied sapsucker	Forest / Positive	Quadratic
American goldfinch	Shrubland / Negative	Linear
Brown-headed cowbird	Shrubland / Negative	Linear
Cedar waxwing	Shrubland / Negative	Linear
Common yellowthroat	Shrubland / Negative	Linear
Eastern towhee	Shrubland / Negative	Linear
Magnolia warbler	Shrubland / Negative	Linear
Northern cardinal	Shrubland / Negative	Linear
Prairie warbler	Shrubland / Negative	Linear
Ruby-throated hummingbird	Shrubland / Negative	Linear
White-eyed vireo	Shrubland / Negative	Linear
White-throated sparrow	Shrubland / Negative	Linear
Chestnut-sided warbler	Shrubland / Negative	Quadratic
Gray catbird	Shrubland / Negative	Quadratic
Indigo bunting	Shrubland / Negative	Quadratic
Mourning warbler	Shrubland / Negative	Quadratic
Yellow-breasted chat	Shrubland / Negative	Quadratic
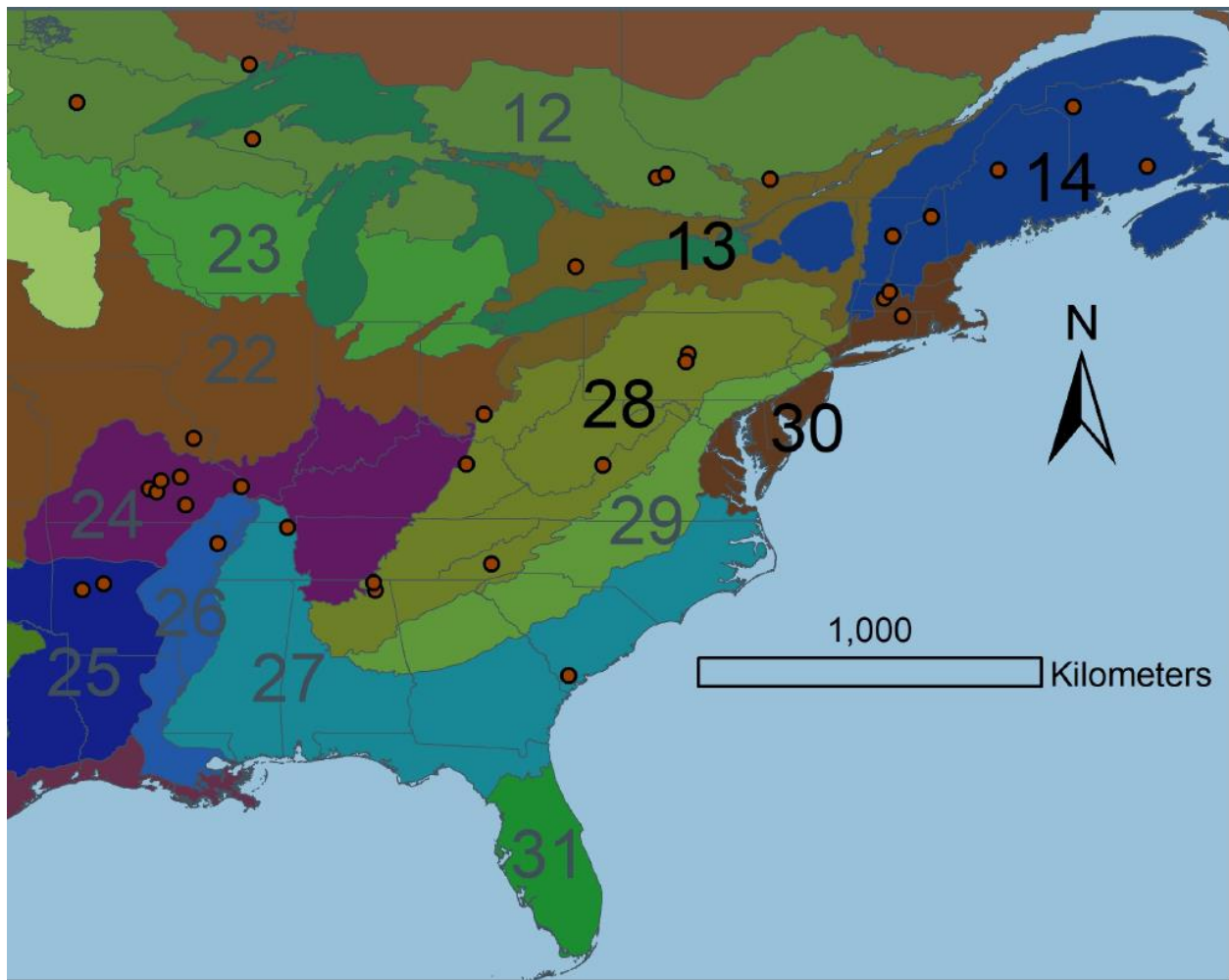
Figure 1. Map of Bird Conservation Regions (BCRs) in eastern North America with points denoting the approximate location of primary studies used in our mature-forest or shrubland bird (Akresh et al. 2021) meta-analyses (GIS locations obtained from the Lott et al. 2019 systematic map). Different colors denote different BCRs, with BCR numbers in black of the four focal BCRs examined in this study.
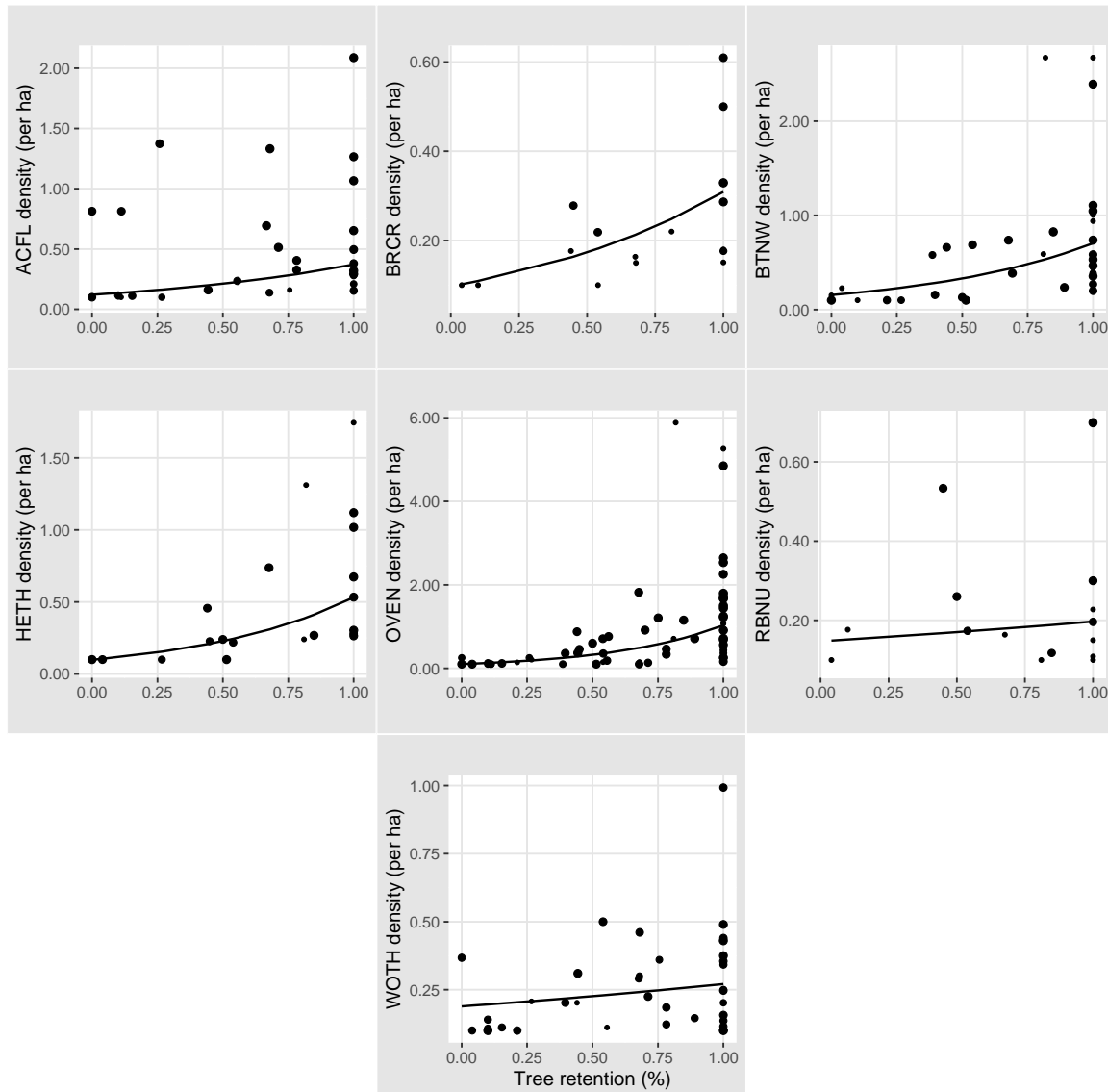
Figure 2. For mature-forest species where a linear predictor was the best fit, we present the effect of tree retention on avian density. Points indicate bird density values from individual studies, and larger points indicate that the data point had a higher weight in the model. Lines and grey shading represent the weighted regression curves and 95% confidence intervals. To fit the models to Gamma distributions, all bird abundances had a small number of 0.1 added to them (so the lowest possible density was 0.1). ACFL = Acadian flycatcher, BRCR = brown creeper, BTNW = black-throated green warbler, HETH = hermit thrush, OVEN = ovenbird, RBNU = red-breasted nuthatch, WOTH = wood thrush.
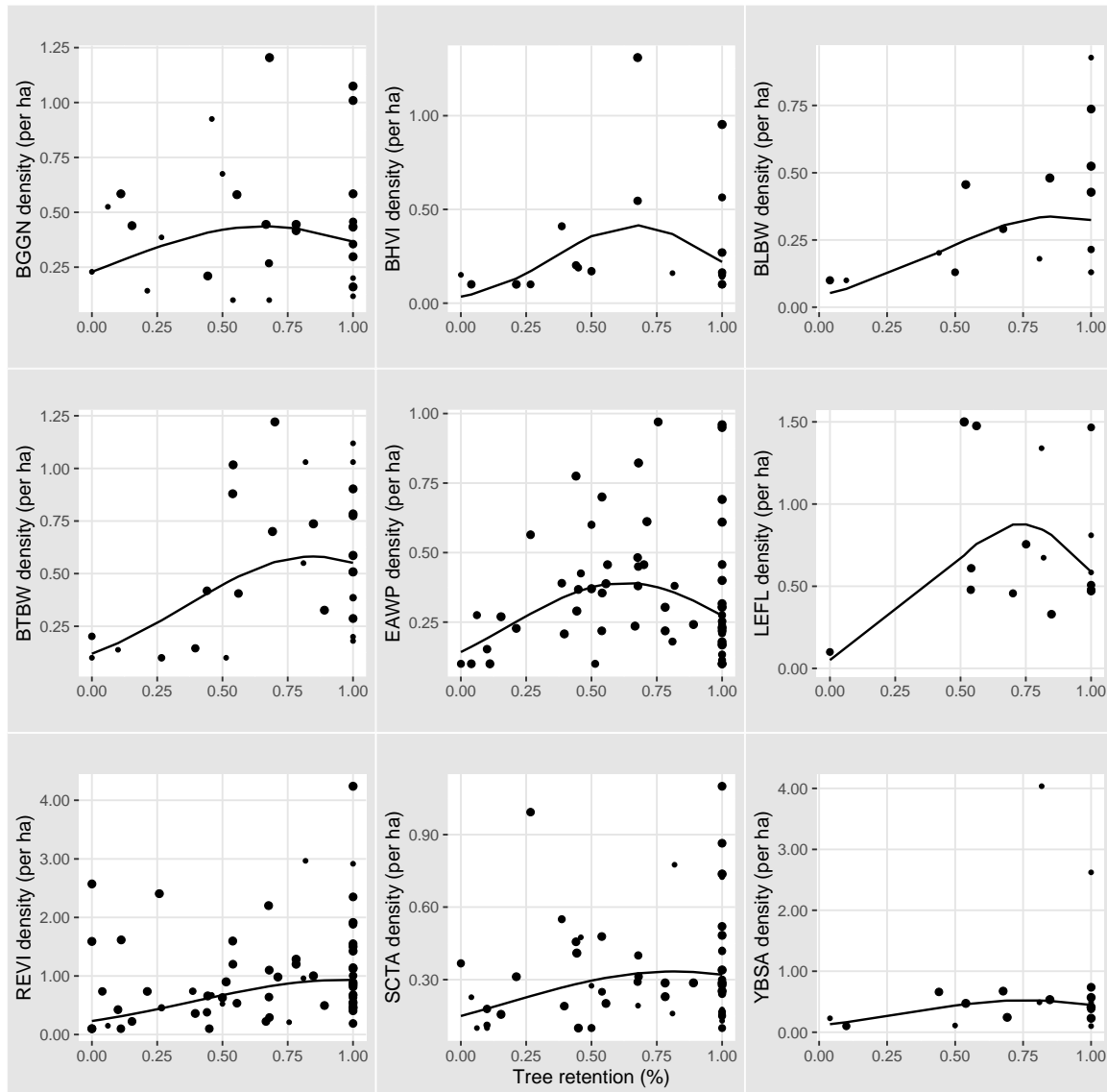
Figure 3. Relationships for mature-forest species in which the quadratic model was the best fit. BGGN = blue-grey gnatcatcher, BHVI = blue-headed vireo, BLBW = blackburnian warbler, BTBW = black-throated blue warbler, EAWP = eastern wood-pewee, LEFL = least flycatcher, REVI = red-eyed vireo, SCTA = scarlet tanager, YBSA = yellow-bellied sapsucker.
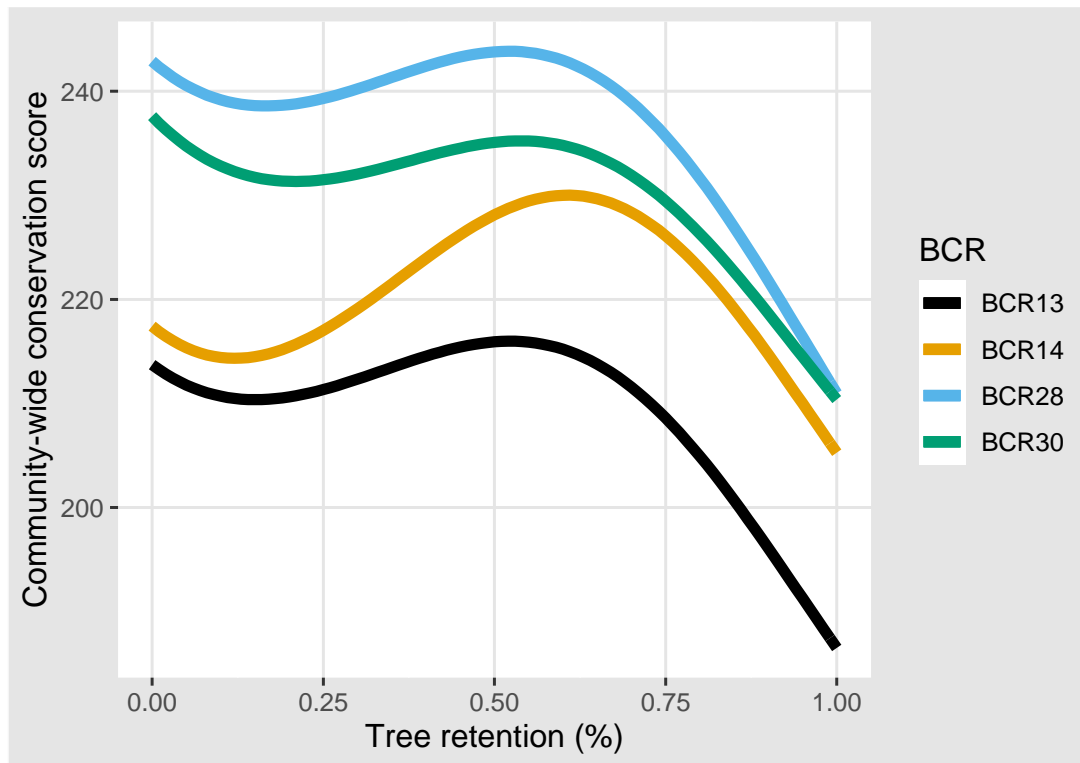
Figure 4. Community-wide conservation scores as a function of tree retention for BCRs 13, 14, 28, and 30.
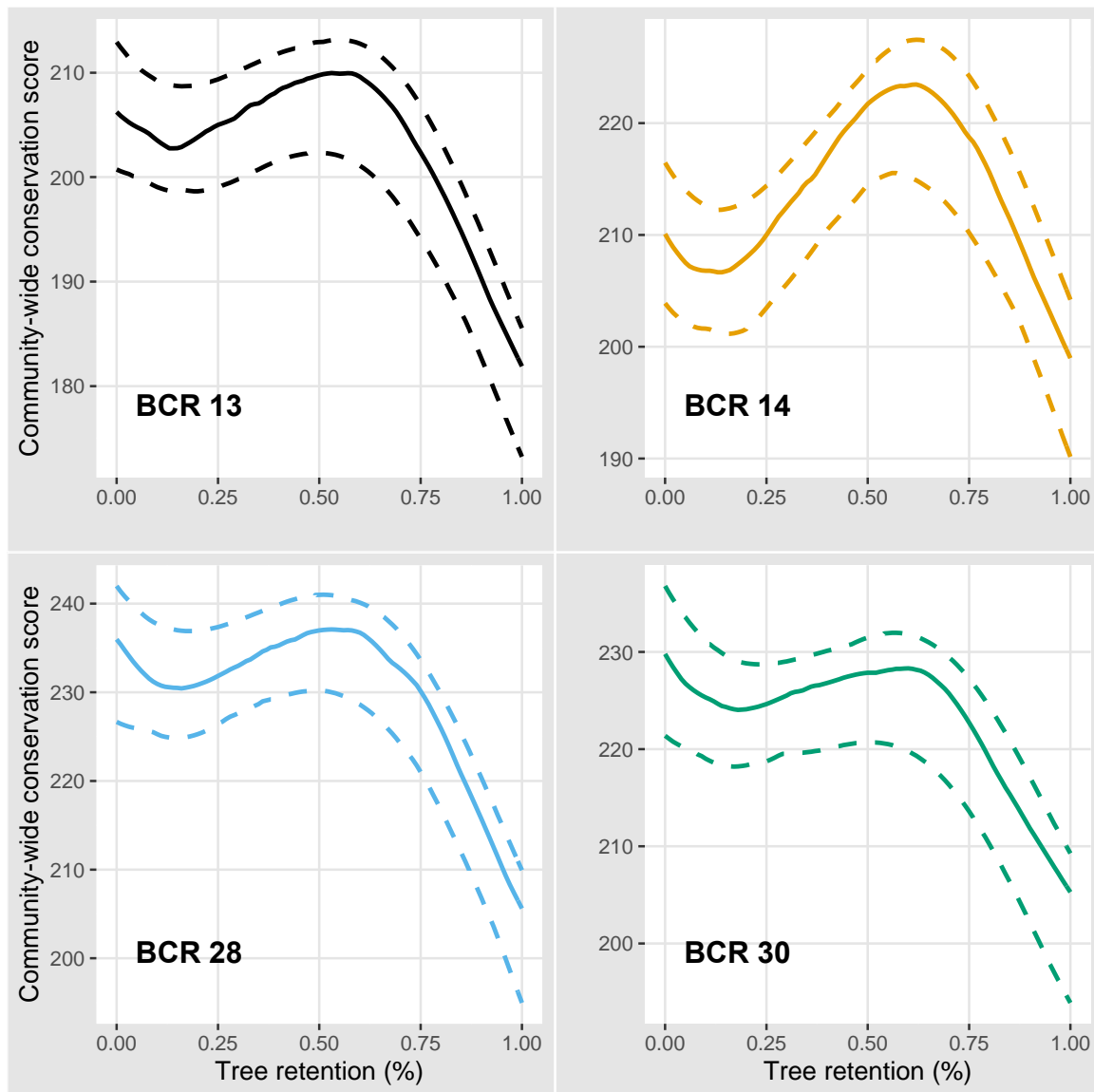
Figure 5. The median and 95% confidence intervals of community-wide conservation scores after conducting a jackknife analysis by iteratively removing individual species from the calculations, and then plotting as a function of tree retention. Shown are separate relationships for each BCR.
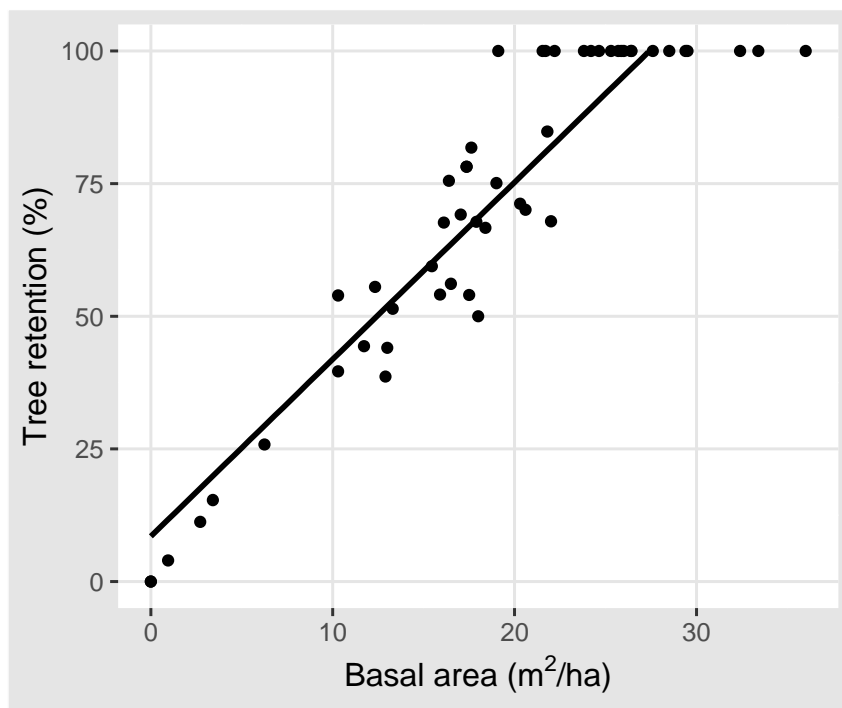
Appendix Figure 1. Relationship between the actual basal area recorded in different treatment levels within a study and percent tree retention. Unmanaged forest stands were classified as 100% tree retention, while tree retention percentage for harvested stands were based on the proportion of the basal area of the unharvested forest stand in a given study.
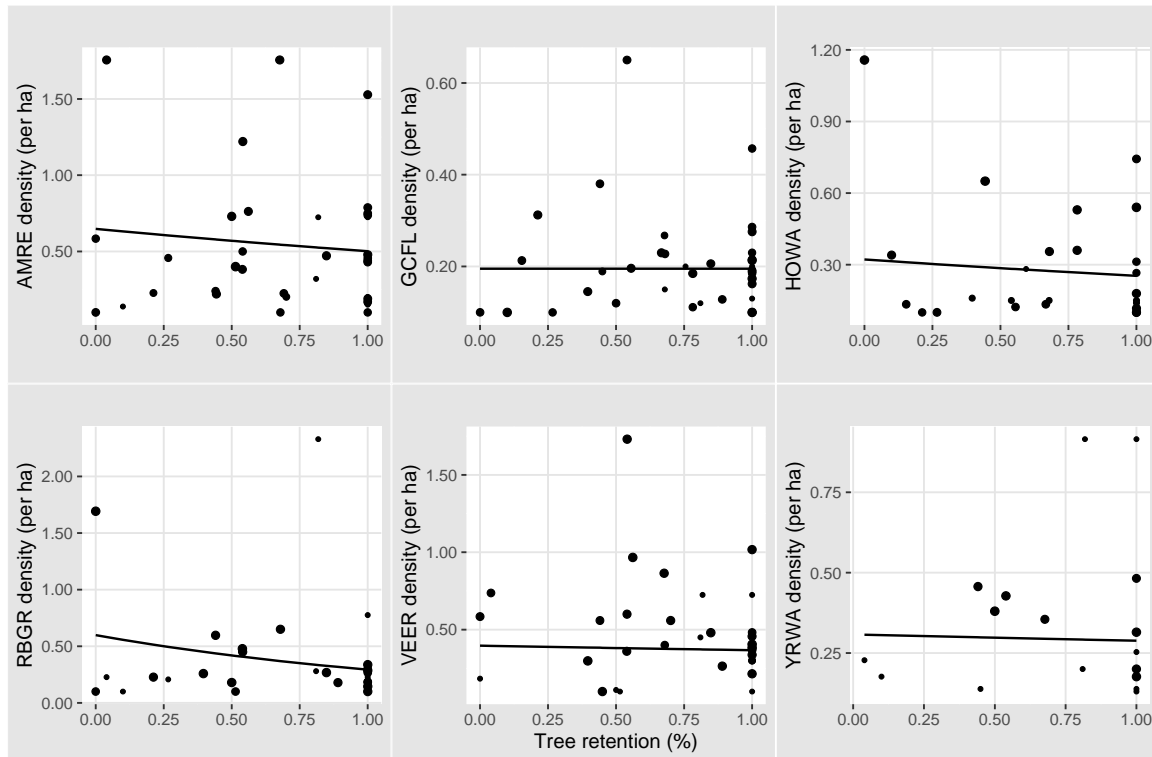
Appendix Figure 2. Figures for putative mature-forest species in which there was no relationship between a continuous variable of tree retention and bird density. American redstart (AMRE) and great-crested flycatcher (GCFL) had 37 data points from 16 studies, hooded warbler (HOWA) had 25 data points from 10 studies, veery (VEER) had 32 data points from 13 studies, and yellow-rumped warbler (YRWA) had 17 data points from 8 studies.

III. A Meta-Analysis of Edge Effects on Nesting Success in Forest and Shrubland Birds of Eastern North America

Summary: In Eastern North America, populations of shrubland and mature forest birds are in decline. Numerous studies report edge effects decrease avian reproductive success, yet variation among species, sites, and nesting guilds obscures overall patterns. We performed a meta-analysis to examine the effects of edges on shrubland and mature forest bird nest survival. Our literature review identified 19 studies that conformed to our search criteria, which included nest survival data for 11 shrubland species and 9 mature forest species. Our results show that nest success for mature forest birds declines as nests are placed closer to edges, when accounting for random effects of species and study. We did not find a significant effect for shrubland birds. We also examined interactive effects of edge type and landscape composition on nest survival, but found no significant relationships with these variables. Single-species analyses showed a relationship between distance to edge and nesting success for hermit thrush (Catharus guttatus). Although we observed a significant effect for mature forest species and not for shrubland birds, our observations could be the result of mature forest specialists nesting farther from the edge compared to shrubland birds; all but three shrubland bird data points were within the first 100 meters of an edge. Thus, both mature forest and shrubland specialists may be facing higher nest predation at edge environments, but the impact of edges is only recognized for forest species that also nest far from edges. More studies are needed on nest survival in large shrublands (where nests are far from edges). Additionally, full-season productivity metrics would be useful to completely comprehend the effects of edges. Nonetheless, previous literature and our findings suggest that managers and conservationists should consider edge effects in evaluating habitat management practices, favoring larger patches that have core areas farther than 200 m from edges.

Introduction

Avian populations are vulnerable to changes in their nesting habitat, including alterations in vegetation cover, predation exposure, and noise interference (Manolis et al 2002, Batary and Baldi 2004 and Thompson 2007). Specifically, the existence of an edge environment such as a road, agricultural field, or silvicultural harvest can have an effect on the seasonal productivity of nesting birds (Flaspohler et al 2001a, Woodward et al 2001). Avian nest predators, such as blue jays (Cyanocitta cristata) and raccoons (Procyon lotor), tend to increase in abundance and activity near edges, leading to lower nest survival relative to interior sites (Barding and Nelson 2008, Chalfoun et al. 2002, Donovan et al. 1997). Thus, effects of edges on nesting success should be considered when looking at long term viability of both shrubland and mature forest birds (King et al 2009, Robinson et al 1994, Donovan et al 1995).

Current understanding of how birds' nesting success is affected by edges is derived from individual studies performed at distinct study sites often with a singular edge type (Friesen et al 1999, Woodward et al 2001 and Burke and Nol 2000). Primary studies usually only focus on one or a few bird species (e.g., Moorman et al. 2002, Kaiser and Lindell 2007), so making general inferences from these studies about edge effects on the entire bird community is difficult. Furthermore, there is extensive variation in the strength and importance of edge effects on nest survival among studies conducted at different sites, even within the same species (King et al. 2001, King and Byers 2002, King et al. 2009).

Meta-analyses are an important tool for synthesizing findings from multiple studies (Arnqvist and Wooster 1995); yet prior meta-analyses on the effects of edges on nest success include both natural nests as well as artificial nests, and combined results across all species (Paton 1994, Hartley and Hunter 1998, Lahti 2001, Stephens et al. 2003, Batary and Baldi 2004). Since artificial nests lack the presence and activity of adults and young that serve as cues for predators, these studies may not effectively indicate the effects of edges on predation of actual nests (King et al. 1999, King and DeGraaf 2006, Thompson and Burhans 2004). Artificial nests may have lower survival rates than natural nests (Smith and Hayes 2002 and Burke et al. 2003) and may not exhibit seasonal or temporal variation in nest survival (Buler and Hamilton 2000, Burke et al. 2003). Previous meta-analyses also examined all bird species and communities together, sometimes across ecosystems worldwide (e.g., Batary and Baldi 2004). Combining across species and ecological communities may be valuable for illustrating overall effects, but can fail to incorporate differences among bird communities, specific regions, or individual species, with respect to the impacts of edges on nesting success (Flaspohler et al. 2001b). Additional variation, such as edge type (Suarez et al. 2003) and landcover surrounding primary habitat (Driscoll and Donovan 2004), can also influence edge effects and should be accounted for in analyses.

We performed a meta-analysis examining the effects of distance to edge and interactions with edge type and landscape composition on nesting success of forest and shrubland birds in the eastern U.S. to synthesize existing data in this region. We separately examined forest and shrubland bird communities, as well as individual species. Our quantitative relationships presented here can be used as a tool for forest managers and conservationists to better manage the needs of both forest and shrubland birds.

Methods

We selected bird species based on a review of avian habitat preferences and included all birds that typically breed in shrubland and forested habitats in eastern North America (Annand and Thompson 1997, King and DeGraaf 2000, Schlossberg and King 2007, Lott et al. 2019). We only examined and included studies in Eastern North America, which is an ecologically cohesive area bounded to the west by the Great Plains, and defined by the United States Forest Service (USFS) regions R8, R9 and eastern Canada (King and Schlossberg 2014).

Data for our meta-analysis came from studies that analyzed nest survival for individual forest and shrubland in relation to nest distance to edge. Relevant studies were found by searching published papers on Web of Science, Academic Search Complete, OAlster, Oxford Scholarship Online, Taylor and Francis Journals, WorldCat.org and Google Scholar. We searched with the following key phrases: "edge", "nest success", "species specific", "nest survival", "distance to edge", "daily nest survival", "eastern North America" and/or "avian". Additional studies were found by consulting an ongoing systematic map of forest bird species-environment relationships (Lott et al. 2019). We also used 'snowballing' techniques to search for studies (Wohlin, C 2014). For example, we reviewed article 'Cited by' lists in Google Scholar, relevant meta-analyses and primary source studies to find additional publications (Vanderwel et al. 2007, Verschuyl et al. 2011, Fontaine and Kennedy 2012, Lahti et al 2001 and Stephens et al 2004).

We collected data from each study, including the year of the study, edge type, and location. We only examined studies that presented species-specific nest survival data in discrete distance-to-edge bins (e.g., 0-50m from an edge, 50-100m from an edge). For each bird species and distance-to-edge bin within each study, we recorded the nest survival or depredation rate

(including daily nest survival, daily nest predation, percent of nests that failed, or percent of nests that survived; depending on the study) and the number of nests. Most studies had data presented in tables, although some of the studies we used Web Plot Digitizer Version 4.1 (Rohatgi 2018) to obtain data from figures. Studies that did not have data on daily nest survival or nest success or discrete distance-to-edge categories were excluded. We also excluded studies that had only artificial nest data or only community- or guild-survival rates.

Given that studies presented daily survival rates, nest survival during a given nesting cycle, or other nest survival metrics, and used a variety of methods to analyze nest success, we standardized the data to the best of our ability to be able to compare survival rates. All survival rate metrics were converted (if necessary) to nest survival during a given nesting cycle. To convert daily nest survival into nest survival during a given nesting cycle, we obtained nesting interval length in days for each species of interest. We consulted Cornell Lab's Birds of the World (Birds of the World, 2020), and for each species in the study, summed the number of laying days, incubation days, and nestling days. We then calculated the nest survival for a nesting cycle with the following equation; $NS = DNS^{\#nesting\ days}$.

Distance to edge values were standardized using midpoints of the distance-to-edge bins within each study. For instance, if the original study had a distance to edge bin of 100-200 m for a set of nests, the midpoint we assigned to the nests was 150 m. When the distance to edge bins were open ended (e.g., > 200 m from the edge), we reached out to the original authors of the study in an attempt to determine the end of the range. For the small percentage of data points that we were unable to determine the farthest distance from the edge in a given study (10 %), we used an estimated midpoint value by adding 50 m to the start of the bin (e.g., > 200 m from the edge was assigned a midpoint distance-to-edge value of 250 m).

We also computed the amount of forest and agricultural land cover adjacent to each study area using ArcGIS. We created polygons of each study site based on the geographic locations described in each paper. To determine adjacent land cover, we used the National Landcover Database raster dataset (MRLC, 2018) and the land cover dataset from Natural Resources Canada (Canada, 2020). We classified adjacent land cover as a 1km buffer of the study site. We then obtained the portion of landscape types within the buffer polygon. We classified the following landscape types as forest for the US Database; Deciduous Forest, Evergreen Forest, Mixed Forest, Scrub/Shrub and Herbaceous, Hay/Pasture and Cultivated Crops were classified as agriculture. We explored including study site with the 1 km buffer and achieved similar results, therefore we decided to use simply the buffer polygons in presented results. The forest and agricultural land cover variables were highly correlated, so we just examined percent forest cover in our analyses.

All studies were also classified by type of edge by reviewing the method sections of each primary source. Based on descriptions in the study, we classified edge type for each of our data points as either 1) Silvicultural edge (e.g., clearcut versus mature forest), 2) Road edge, or 3) Agricultural edge.

Data Analysis

We primarily examined published data that could be directly used in our meta-analysis, but to increase sample sizes, we also used three raw datasets from studies that had nest survival data but did not previously examine the data with distance to edge bins (Akresh 2012, Akresh and King 2016, and King et al. 2009). Using these raw datasets, we first analyzed the effects of distance to edge in categorical bins on daily nest survival for individual species using the program MARK through the R package "RMARK" (Laake J, 2013). A model was run for any

species with more than ten nests in each raw dataset that was used. Distance to edge bin sizes were selected to encompass a suitable number of nests per bin for nest survival analysis and varied by each raw dataset. For Akresh (2012), we used bins of 0-10m, 10-20m, 20-50m, 50-100, 100-250; for King et al. (2009), we used bins of 0-10m, 10-20m and 20-50m; and for Akresh and King (2016) we used bins of 0-50m and 50-250m due to small sample size). When conducting the nest survival models, our predictor variable was the categorical variable of distance to edge bins, with the response variable of daily nest survival. The daily nest survival values per bin obtained from these models were then included in the overall meta-analysis dataset and standardized, similar to data from other studies.

Nest success values for each species within a study were weighted based on the number of nests and the range of the distance to edge bin. We first computed a weight based on the number of nests for each species (Wn): less than 10 nests in a distance-to-edge bin were assigned a Wn of 0.33, between 10 and 30 nests a Wn of 0.66, and more than 30 nests were weighted 1. Our second weight metric (We) attempted to weight how well the midpoint of the distance to edge bin was actually reflecting the distance to edge. We were determined by proximity to edge and width of the distance to edge bin. Any distance to edge bin recorded in studies that was greater than 150 m from the edge (e.g., 150-300 m, 200-400 m, etc.) was given a weight of 1. As observed in the primary literature, the midpoint of these distance to edge bins could be considered interior habitat and therefore was given the highest weight (Burke and Nol 2000, Driscoll and Donovan, Flaspohler et al 2001). However, although midpoints of a distance to edge bin of 50-100 m and a distance to edge bin of 0-150 m are both 75 m, these bins differ in precision. Especially for distance-bins close to edges (< 150 m from the edge), bins with low precision may be less useful in assessing edge effects. Thus, for We, data with 50 m bin widths or smaller were weighted 1, data with 50-100 m bin widths were weighted 0.66, and data with a 0-150 m range were weighted 0.33. To obtain an overall weight for each data point (Wo), we multiplied the number of nests weight by the distance to edge weight (Wo = Wn x We).

We fit generalized linear mixed models (GLMMs) separately for each bird species guild (forest and shrubland) and for each species with at least 10 data points. Daily nest survival values were highly correlated with our standardized nest success metric (nest survival during a nesting cycle; r2 = 0.91). We chose to use the latter as the response variable because these values better fit a normal distribution. We also included a random effect of study (Zuur et al. 2009), which allowed us to account for various sampling methods, geographical location, and design of different studies. We used weighted regression models; therefore, each data point was weighted via the aforementioned weight classifications. We examined models separately for forest vs. shrubland bird species because during exploratory analyses, we found a significant interaction between bird species guild (forest/shrubland birds) and distance to edge on nest survival (p = .0298).

We ran six models in our candidate model set for each bird guild. Akaike's information criterion corrected for small sample sizes (AICc) and Akaike's model weights were used to compare the models and determine influence of distance to edge, edge type, or landscape on nest success (Burham and Anderson 2002). We fit a null mixed linear model that showed weighted standardized nest success and accounted for random effects of study and species. Five mixed linear models explored weighted standardized nest success with edge midpoint fixed on the x axis and the addition of landscape values as variables. Interactions between edge midpoint and landscape type and between edge midpoint and edge type were included in two of the models. A final global model encompassed all potential variables with landscape, edge midpoint and edge

grouping. We defined the top model for each guild as the model with the lowest AICc value and presented model parameters and significance values from mixed effects models.

In addition to examining effects of edges on specialist groups we were also interested in models with distance to edge as a predictor variable for individual species. As before, edge midpoint was fixed on the x axis and landscape values were added as variables. If there were less than five studies in the species data set, as was the case with hermit thrush, indigo bunting, prairie warbler and rose-breasted grosbeak, we did not include the random effect of study, and instead used a fixed effect (Harrison et al. 2018). Two species had more than five studies in the dataset, wood thrush and ovenbird, therefore we included a random effect of study (see table 1 for scientific names). Analyses were conducted using the R statistical program version 3.4.3 (R Core Team 2020), lme4 and lmerTest packages were used to conduct mixed-effect models (Bates et al. 2015, Kuznetsova et al. 2016).

Results

In total, 62 manuscripts were downloaded and reviewed, of which 19 studies fit our selection criteria. We found data on 20 bird species, including 11 shrubland species and 9 forest bird species. We acquired enough data to fit models for two specialist groups (forest and shrubland) and six individual species.

The forest specialist's dataset included 88 data points from 12 studies; model 1 was the top model, and none of the other models were within 2 AICc values (Figure 2). Model 1 had a significant relationship with the response variable and the highest weight at 0.83. The model included edge midpoint as the response variable. The shrubland specialist's dataset included 48 data points from 8 studies; the null model was top model; therefore, no predictor variable had a significant relationship with the response variable (Figure 1).

For individual species analyses there were significant results for one forest specialist when study was kept as a fixed effect and a linear model was run. Hermit Thrush (Figure 3) showed a positive trend of increasing nest success as distance to edge increased. The other five species (ovenbird, wood thrush, indigo bunting, prairie warbler and rose breasted grosbeak) did not have any significant relationship to the edge.

Discussion

Through this meta-analysis of studies across eastern North America, we found that forest bird nest success increases as distance to edge increases, but shrubland specialists did not exhibit the same trend. These findings on forest birds are consistent with previous individual studies that have found edges can impact nest survival, and nest proximity to edge may indicate less suitable habitats for certain avian species (King et al 1996, Friesen et al 1999, Flaspohler and Temple et al 2001). For shrubland birds, our meta-analysis complements the individual studies that have found varied and inconsistent results of the effect of edges on nest survival (e.g., Woodward et al. 2001, Burhans et al. 2002, Weldon and Haddad 2005).

Elevated nest predation rates near edges may be due to lower numbers or activity of predators within interior forests and under increased canopy cover (Marini et al 1995, Zanette et al 2000). Researchers have also seen an increase of certain nest predators at edge environments, including small mammals such as chipmunks and squirrels, as well as snakes (King et al. 1998, Chalfoun et al 2001, Weatherhead and Charland 1985). An increase of predators may be more prevalent in certain abrupt edges which have high predation rates, while gradual edges have less predation attempts (Suarez et al 1996). Predators might be more abundant near edges because they favor open habitats and spill over into adjacent forest edges, or forest edges might focus

predator activity; for instance, predators might use resources in openings and forest, resulting in concentration near edges (King et al. 1998).

One potential reason nest predation on shrubland birds was unrelated to distance from edges was because most of the shrubland nests in our study were found within 50 m of an edge, and were thus within an area of high predation risk. Few shrubland species nested greater than 50 m from the edge and therefore, any analysis on more interior nest success for these birds was not possible. After conducting a post-hoc analysis to examine overall nest success for forest and shrubland birds, shrubland specialist nesting success was cumulatively lower at 0.413 than forest birds nest success at 0.534. This lower nest success in shrubland specialists is consistent with the view that their nesting closer to the edge than interior specialists makes them more prone to more edge effects such as regular predation attempts (Shake et al 2011, Morris and Conner 2016). This could indicate a higher vulnerability of shrubland birds due to their habitat use. However, other reasons may also be possible for the lack of edge effects on shrubland birds, such as increased small mammal abundance or increased activity of other predators that are found throughout shrubland habitats (Fantz and Renken 2005, Schlossberg and King 2007, Akresh et al. 2017).

The ground nesting hermit thrush showed a significant increase in nest success as distance to edge increased, consistent with past studies on this species (Flaspohler et al 2001b, Manolis et al 2002). The other individual species analyses did not show a significant trend in nesting success relative to edge distance, although negative edge effects for ovenbirds were marginally significant (p = 0.079). Notably, both of these species are ground nesters, which in a multi-species analyses of nest success with respect to clearcut edges, Flaspohler et al. (2001b) reported were more vulnerable to edge effects than above-ground nesters, as we found in our study. Many forest bird studies have noted a decrease in nest success at edges and have hypothesized nest height and understory cover may determine nest vulnerability. The specific requirements of these habitat characteristics will vary based on species (Newel and Kostalos 2007, Woodward et al 2001), making some species more vulnerable to edge predators than others.

It should also be acknowledged that concerns have been raised against using nest success values as a sole indicator of productivity (Donovan et al 2008, Jones et al. 2005, and Thompson et al. 2001). Nest survival only examines a single nesting cycle and does not take into account any re-nesting attempts after nest failure. Additionally, our study does not consider post-fledging survival, an important metric of seasonal fecundity (Cox et al. 2014, King et al. 2006, Streby and Anderson 2011). We acknowledge that these are potential concerns. Unfortunately, relatively few studies have examined full-season productivity measures in relation to edges, and we did not find enough studies to conduct a meta-analysis on full-season productivity. The few studies that have looked at edge effects and full-season productivity have found an increase in productivity with a reduction of edge habitat in some species (Peterson et al 2015) but for others, edge habitats may increase survival of post-fledging birds (Jenkins et al 2016, King et al 2006). This indicates that post-fledging habitat selection and success can vary from nest habitat and success depending on the species, though more research is needed (Adalsteinsson et al 2018, Jenkins et al 2016).

Through our literature review we found many studies that were relevant to our research but were not included because they used a continuous effect of edge distance or grouped species for analysis. Our study results were similar to studies that looked at a continuous effect of distance to edge on nest survival, because several found that predation decrease as distance to edge increased, or nest survival increased as distance to edge increased (Weldon 2006, Vargas

and Robinson 2005, Chapa-Vargas et al 2013). Results from the studies that grouped species were more variable, but some found an increase in nest success as distance to edge increased in shrubland birds or open cup nesters (Shake et al 2011), while others found no effect (Hanski et al 1996, Duguay et al 2001).

We did not find potential interactive effects between landscape forest cover or edge type and distance to edge on nest survival, which contrasts with some individual studies (Suarez et al. 2003, Driscoll and Donovan 2004, Cox et al. 2012). Across sites and geographical locations in eastern North America, perhaps predator abundance or activity does not vary among the edge types we examined in our study. For effects of landscape forest cover, most of the studies (68%) we included in our analyses had forest cover percentages of >50% in the landscape. Our dataset therefore may not have had enough variation in landscape forest cover to detect differences observed in previous individual studies.

Conclusion
Disturbance through anthropogenic activities such as agriculture, silviculture or development, or natural disturbances, can greatly impact breeding avian species by creating edge environments. This impact will vary based on species specific habitat preference and nesting behavior (King et al. 2006, Batary and Baldi 2004). The significant effect that we observed of forest specialists and their relationship to distance to the edge compared to the lack of effect for shrubland birds may be due to typical nesting location. Forest species also nest far from edges, while all but three shrubland specialist data points were within the first 100 m of an edge. Thus, both mature forest and shrubland specialists may be facing higher nest predation at edge environments. More studies are needed on nest survival in large shrublands to include shrubland nest data further from the edge. Additionally, full-season productivity metrics would be useful to completely comprehend the effects of edges. Nonetheless, previous literature and our findings suggest that forest managers and conservationists should consider the impacts of the amount of edge in a landscape, especially in large interior areas of mature forest, to best sustain bird populations.

Table 1. Studies included in the meta-analysis examining nest survival based on distance to edge in shrubland and mature forest species in Eastern North America.

Study	Location	Years	Landscape	Number of Nests in Study	Species*	Edge Categories (m)
Akresh 2012	MA	2008-2011		265	PRAW	0-10, 10-20, 20-50, 50-100, 100-250
Akresh and King 2016	MA	2008-2013		21	WHIP	0-20, 20-50
Burke and Nol 2000	Ontario	1996-1997	Forest-suburban	298	OVEN, RBGR, REVI, VEER, WOTH	0-50, 50-100, 101-200, >200
Driscoll and Donovan 2004	NY	1998-2000	Agriculture	230	WOTH	0-200, >200
Flaspohler et al 2001a	WI	1995-1998	Forest	90	OVEN	0-300, 300-1000
Flaspohler et al. 2001b	WI	1996-1999	Forest	463	AMRO, BTNW, HETH, OVEN, RBGR, REVI, SCTA	0-100, 101-200, 201-300, 301-400, 401-950
Friesen et al. 1999	Ontario	1996-2002	Agriculture	217	RBGR, WOTH	0-5, 5-25, 25-50, 50-100, >100
Kaiser and Lindell 2007	MI	2002-2003	Agriculture	19	WOTH	100-200
King and Byers 2002	MA	1999-2000	Forest	40	CSWA	0-5, 5-10, 10-15, 15-20
King et al. 1996	NH	1992	Forest	98	OVEN	0-200, 201-400
King et al. 2001	NH	1994-1996	Forest	156	CSWA	0-10, 0-110
King et al. 2009	MA		Forest	199	COYE, CSWA, GRCA, PRAW,	0-10, 10-20, 20-50

					EATO	
Manolis et al. 2002	MN	1992-1998	Forest	349	HETH, OVEN	0-140, 141-274, 275-531**
Moorman et al. 2002	SC	1996-1999	Agriculture	99	HOWA	0-50, 51-100, >100
Robinson and Wilcove 1994	IL	1989	Agriculture	196	ACFL, WOTH	0-99, 100-199, 200-399, 400-800
Streby and Anderson 2011	MN	2007-2008	Forest	185	OVEN	0-100, 100-1356
Suarez et al. 1997	IL		Agriculture	179	INBU	0-50, >50
Woodward et al. 2001	MO		Forest	311	FISP, INBU, PRAW, YBCH	0-20, 21-40, 40-123

*ACFL = Acadian Flycatcher (Empidonax virescens), AMRO = American Robin (Turdus migratorius), BTNW = Black-throated Green Warbler (Setophaga virens), COYE = Common Yellowthroat (Geothlypis trichas), CSWA = Chestnut-sided Warbler (Setophaga pensylvanica), EATO = Eastern Towhee (Pipilo erythrophthalmus), FISP = Field Sparrow (Spizella pusilla), GRCA = Gray Catbird (Dumetella carolinensis), HETH = Hermit Thrush (Catharus guttatus), HOWA = Hooded Warbler (Setophaga citrina), INBU = Indigo Bunting (Passerina cyanea), OVEN = Ovenbird (Seiurus aurocapilla), PRAW = Prairie Warbler (Setophaga discolor), RBGR = Rose-breasted Grosbeak (Pheucticus ludovicianus), REVI= Red-eyed Vireo (Vireo olivaceus), SCTA = Scarlet Tanager (Piranga olivacea), VEER = Veery (Catharus fuscescens), WHIP = Eastern Whip-poor-will (Caprimulgus vociferous), WOTH = Wood Thrush (Hylocichla mustelina) and YBCH = Yellow-breasted Chat (Icteria virens). ** Maximum distance to edge of a nest in this study was obtained from author communication

Table 2: Shrubland Specialist Mixed Effects Weighted Linear Models

Model Variables	K	AICc	ΔAI	Wi
Null	3	-27.69	0	.96
Distance to Edge midpoint	4	-20.06	7.63	.02
Distance to Edge midpoint + % forest cover in landscape	5	-18.66	9.03	.01
Distance to Edge midpoint * % forest cover in landscape	6	-15.49	12.21	0
Edge type + Distance to Edge midpoint	6	-15.41	12.28	0
Distance to Edge midpoint + % forest cover in landscape + Edge type	7	-13.79	13.90	0
Edge type * Distance to Edge midpoint	8	-9.82	17.87	0

Table 3: Forest Specialist Mixed Effects Weighted Linear Models

Model Variables	K	AICc	ΔAIC	Wi
Distance to edge midpoint	4	-52.40	0	.83
Distance to edge midpoint + % forest cover in landscape	5	-48.20	4.2	.10
Null	3	-46.46	5.94	.04
Distance to edge midpoint * % forest cover in landscape	6	-44.31	8.08	.01
Distance to edge midpoint + Edge type	6	-43.19	9.21	.01
Distance to edge midpoint * Edge type	8	-40.67	11.83	0
Edge type + Distance to edge midpoint + % forest cover in landscape	7	-38.85	13.55	0
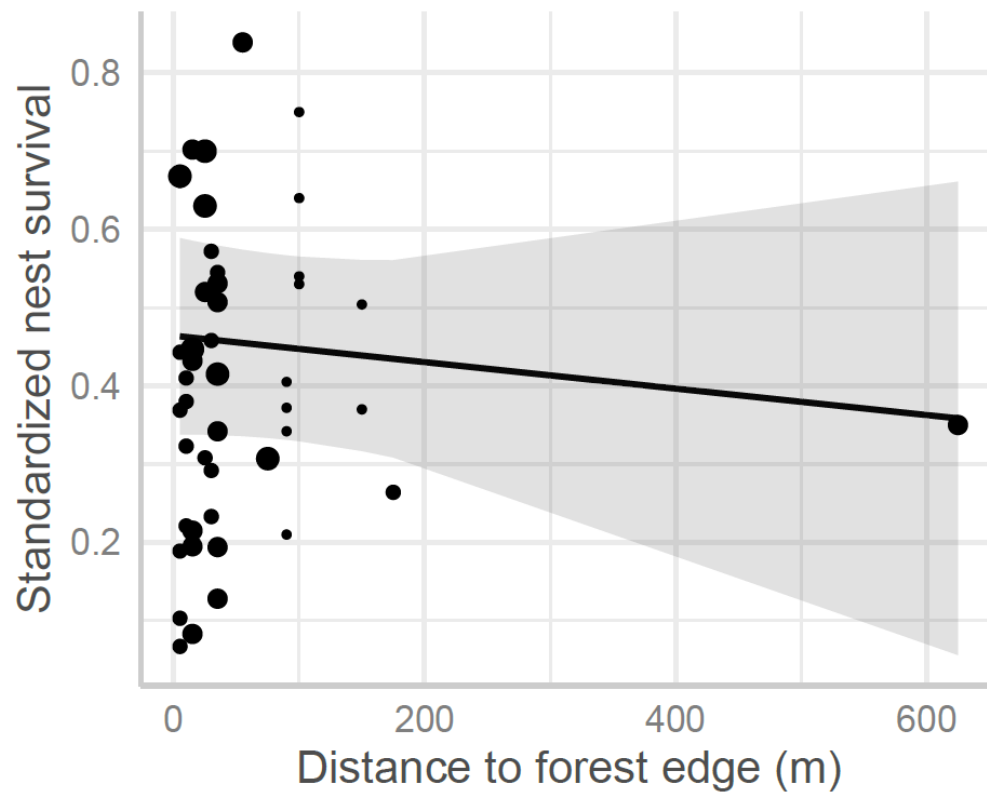
Figure 1.

Shrubland Birds Nest Survival in Relation to Distance from Forest Edge
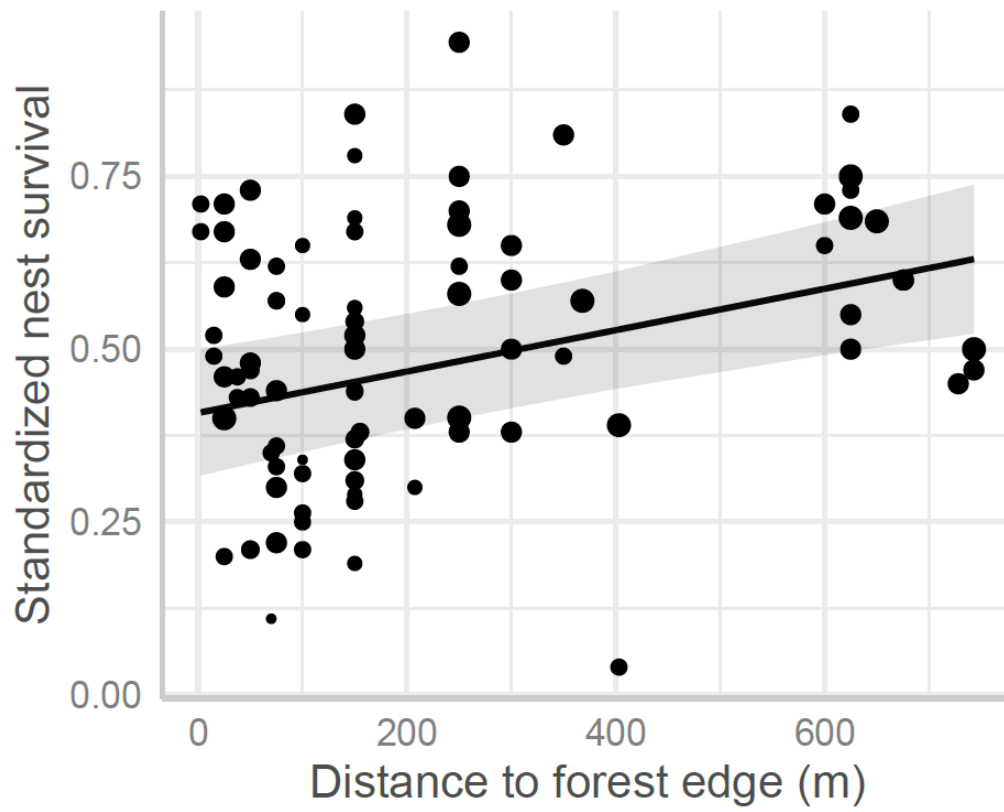
Figure 2. Forest Birds Nest Survival in Relation to Distance from Forest Edge
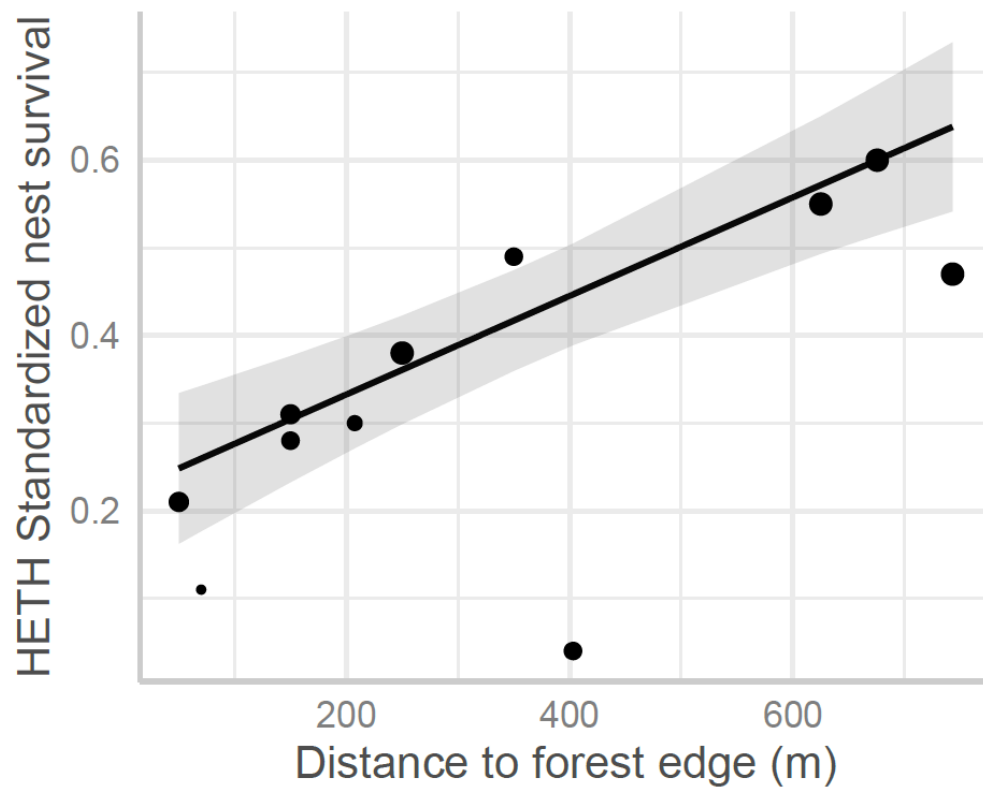
Figure 3. Hermit Thrush Nest Survival in Relation to Distance from Forest Edge

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IV. **Bridging the gap between science and land managers: A case study on the development of the Predictor of Avian Communities Tool (PACT)**

Summary: As a result of the continued loss of early-successional forest habitat across the United States, many native shrubland bird populations are declining. Forest management can help maintain shrubland bird populations and is therefore critical to preserving overall avian diversity in New England. The Predictor of Avian Communities Tool, or PACT, is an open source, web-based decision support tool developed by the U.S. Forest Service Northern Research Station to enable land managers to create early-successional habitat and increase shrubland bird biodiversity in locations across the eastern U.S. This case study describes the development process of this decision support tool and, using published best practice recommendations, examines its strengths and weaknesses. These recommendations will help managers understand the potential and limitations of this tool, provide guidance for improvements to PACT, and support the development of other web-based decision support products to help bridge the research-implementation gap in shrubland bird management.

Introduction

Historically, forests in the northeastern United States were shaped by natural and anthropogenic disturbances such as fire, wind, flooding, and agriculture that continuously produced early-successional habitats (DeGraaf & Yamasaki, 2003). However, these disturbance regimes have been altered or suppressed over time, resulting in a drastic decline in the extent of young and early-successional forest habitat in the region (DeGraaf & Yamasaki, 2003). Many species, such as "shrubland" birds, require the conditions and resources present in recently disturbed sites and disappear as succession proceeds (Schlossberg & King, 2014). The loss of early-successional habitats has therefore resulted in a drastic decline in shrubland birds, making the conservation of these species of particular concern to the scientific community. In lieu of the historic disturbances that once supported shrublands and young forest habitats in the northeast, regeneration following a timber harvest has been determined to provide high-quality habitat for disturbance-dependent birds (King & DeGraaf, 2000). Land managers can therefore use specific silvicultural prescriptions to increase the amount and quality of early-successional habitats available for shrubland birds (DeGraaf & Yamasaki, 2003). Due to the rapid rate of succession in the northeast, shrubland habitats must be continuously created to maintain bird populations, but silviculture offers the advantage of offsetting management costs with timber revenue (Schlossberg & King, 2009; Roberts & King, 2017). Silviculture has become a critical tool in supporting shrubland bird habitat in New England, contributing to approximately 78% of early-successional forests in the region (Schlossberg & King 2007).

The vertical structure created by silvicultural openings is key to ensuring their value as habitat for shrubland birds; a number of silvicultural systems create the low, dense shrubby and herbaceous cover these species require. However, vertical structure isn't the only important feature of shrubland habitat – horizontal structure created by patch size also influences habitat value. Many shrubland birds are only encountered in larger patches created by even-aged silvicultural techniques like clearcutting (Costello, et al. 2003), with abundance increasing in correlation with gap size (Annand & Thompson, 1997; Roberts et al., 2017). Group selection harvest is the only uneven-aged practice that has been shown to create suitable habitat for shrubland birds (Annand & Thompson, 1997), but the resulting patches can be too small to support area-sensitive shrubland bird species (Costello et al., 2000).

In addition to patch size, the residual basal area of trees in a stand affects the quality of early-successional habitat. There are significant differences in both vegetation structure and bird abundance among mature forests, shelterwoods, and clearcut habitats, with bird species diversity and richness being highest in shelterwood stands; however, some obligate shrubland species are only present in stands with little or no residual canopy (King & DeGraaf, 2000).

Lastly, land managers must also consider time between treatments given the rapid rate of succession in the northeast. Canopy closure occurs roughly 20 years after a clearcut, causing shrubland habitat in the understory to be shaded out and shrubland species to disappear, so vegetation should grow for 10-15 years before another silvicultural treatment is applied to return openings to an earlier successional stage (Schlossberg & King, 2009).

When discussing the conservation of early successional communities through the application of silvicultural prescriptions, it is important to acknowledge that this management objective can conflict with other goals, such as the conservation and enhancement of biologically mature forests (King & Schlossberg, 2014). However, while it is not possible to manage for all species at a given site, research findings have indicated that even-aged management applied under sustainable best management practices does not exclude mature-forest bird species from extensively forested landscapes and may even enhance habitat during the postfledging period (King & Schlossberg, 2014). Furthermore, given that shrubland bird species are experiencing more significant declines than mature forest birds in the northeast region, the application of even-age silvicultural treatments is still warranted to preserve avian biodiversity, despite the potential to incur some habitat loss for mature forest species (King & Schlossberg, 2014).

Decision Support Tools

In order to successfully create shrubland bird habitat in the northeast, land managers must balance numerous technical and social considerations while writing a forest management plan. Although the theory of producing early-successional habitat for shrubland bird species with silvicultural prescriptions is well established and thoroughly researched, the actual implementation of this management strategy is ultimately contingent upon the successful flow of information between the scientific community and practitioners. Traditionally, peer-reviewed publications and synthetic reviews have been a primary conduit for information sharing between scientists and decision-makers, but historically, there has been an emphasis on increasing the supply of scientific information without considering its correlation to user demands (McNie et al., 2007; Cash et al., 2003). The production of science that informs practice is an enduring challenge that has led to a "research-implementation gap," a phenomenon in which the knowledge produced by researchers is not necessarily used to inform policy or practice (Cook et al., 2013; Knight et al., 2008). For example, Fazey et al. (2005) reviewed 547 papers from three prominent conservation journals published in 2001 and found that only 37% of conservation biology studies had high relevance to management. This gap is further exacerbated by factors such as practitioners lacking access to peer-reviewed literature or experiencing difficulties interpreting relevant scientific information (Knight et al., 2008; Pullin & Knight 2005).

Useful scientific information should improve environmental decision making by expanding alternatives, clarifying choices, and enabling decision makers to achieve desired outcomes (McNie et al., 2007). Furthermore, decision makers need to know what actions do or do not work, or how effective a given action has been in achieving their objectives in order for conservation practice to be effective (Pullin & Knight, 2001). In order for practitioners to properly evaluate their practices and select the best approach for a given site, as is necessary for shrubland bird habitat management, they require consistent access to supporting information and

research that is readily available in a usable format, despite the resource constraints that are common within the conservation field (Pullin & Knight, 2003). Additionally, this research must be perceived as salient, credible, and legitimate to both scientists and decision makers in order to cross the knowledge-action boundary (Cook et al., 2013; Cash et al., 2003).

To help surmount this pervasive obstacle, decision support systems (DSS) have become well-established management tools that support decision making in complex systems, acting as an interface between scientists and practitioners (Pullin & Knight, 2003). Within these systems, targeted decision support tools (DST) can enable the customizable exploration of the consequences and impacts of alternative models for a given decision (Wong-Parodi et al., 2020). DSS can also aid the process of structuring and resolving which action to take when the knowledge about the nature and impact of certain issues, and how best to resolve them, is uncertain and contested (McIntosh et al., 2011). This functionality is critical for land managers, who rely on translatable science to inform and guide complex management practices. DST can synthesize the management implications of relevant publications by incorporating the data and functions from multiple studies to create a decision-making framework that is easily accessible and open-source, transcending potential resource constraints and bridging the research-implementation gap.

Introduction to the Predictor of Avian Communities Tool
Despite the high conservation priority of shrubland birds in New England, land managers are often confronted with uncertainty regarding the most effective management practices to support early-successional habitats. In response to this issue, a team of researchers from the U.S. Forest Service Northern Research Station synthesized a large body of published information into a quantitative decision support tool called the Predictor of Avian Communities Tool (PACT). The development of this tool is a reflection of the Northern Research Station's long-term commitment to producing science that supports management. The intent of this tool is that it will, to some extent, substitute for in-person interactions during field trips and consultations that are the preferred means of dissemination but are limited by scheduling or geographic constraints.

Available to the public through an open access, web-based platform, PACT is designed to allow managers and practitioners specify their geographic locality and management footprint, visualize the outputs of habitat management practices, and compare different management scenarios in terms of shrubland bird abundance and species composition on a map-based interface. The primary objective of PACT is to assist land managers with identifying practices that are most likely to achieve their target goals, and to contrast different management scenarios in terms of their value for shrubland bird habitat management. This tool also enables managers to assemble a conservation portfolio of projects to support the full suite of shrubland birds, and to assist with the prioritization of projects for the purpose of allocating or attracting management funds. In addition to responding to the needs of practitioners, feedback was gathered from stakeholders affiliated the Massachusetts Department of Conservation and Recreation

Figure 1. Users can input information specific to any given management opening in the initial "Add Management Opening" window.

(DCR) and Mass Audubon during the development process to help guide PACT's design and functionality.

Within PACT, users are given the option of locating their project site by address, latitude/longitude, or zip code using a "Search Map" feature. After inputting their management location, the user can either draw a treatment area or upload a shapefile, while also noting if there are any large openings nearby. The actual or anticipated residual basal area within the opening and elapsed time since treatment is also customizable within the initial "Add Management Opening" window. Users can then click an "Analyze" button (see Figure 1) to generate a list of species likely to occur in the project area, and which specific species are likely to be present in the management site itself. "Opening Area", "Basal Area" and "Time" sliders at the bottom of the "Analysis Results" window provide users with the opportunity to explore how different scenarios compare in terms of their effect on shrubland birds (see Figure 2).

Leveraging Primary Literature

The obligate and facultative shrubland bird species included in the species pool for PACT were identified in a report by Schlossberg and King (2007). The data and calculations used to produce PACT's functions are derived from two principal sources of information: 1) basemaps of species occurrence which yield the likelihood of any species being present in a given suitable habitat, termed "regional occupancy" (Figure 2), and 2) peer-reviewed published studies yielding quantitative functions that were used to condition the regional occupancy based on opening area, basal area, and time since treatment values specified by the user. Details on these functions and their incorporation into the decision-support framework are described below.

Regional Occupancy
The probabilities for regional occupancy in the PACT tool are acquired from species-specific base maps developed by Stephen Matthews, an ecologist with the U.S. Forest Service's Northern Research Station (Matthews et al., 2011). Statistical models

Figure 2. Example of results window produced by PACT analysis.

of 147 bird species distributions in the eastern U.S. were developed using climate, elevation, and the distributions of 39 tree species to predict contemporary bird distributions. These analyses gave a broad-scale representation of the habitat conditions that are likely to be associated with eastern U.S. bird species, allowing the authors to encapsulate important habitat requirements and identify where habitats may be suitable in the future (Matthews et al., 2011). The values in the

basemap's raster layers are calculated as the mean value of all the pixels that intersect the management opening drawn by the user.

Habitat Occupancy

Shrubland birds are primarily influenced by opening or patch area, the residual basal area of trees in the stand, and the time that has passed since treatment. Therefore, in PACT, habitat occupancy probabilities are calculated as the product of the occupancy for the user-specified patch area, basal area value, and time since treatment as follows: habitat occupancy = opening area * basal area * time since treatment. The following studies provided the foundation for the elements of this calculation:

1. Opening Area: Area requirements and landscape-level factors influencing shrubland birds, by Roberts & King (2017)

Roberts and King (2017) investigated species-specific minimum-area requirements for shrubland bird species capable of occupying the openings created by group selection harvests in New England. The study area spanned approximately 57,000 ha in Franklin and Worcester counties, Massachusetts, with selected openings ranging from 0.02 ha to 1.29 ha that had been harvested between 2006 and 2010. Data were collected from bird surveys, along with vegetation structure and composition measurements. The study found evidence of relationships between occupancy of study species and microhabitat-, patch-, and landscape-level variables. Black-and-white warbler, common yellowthroat, chestnut-sided warbler, eastern towhee, and gray catbird were capable of occupying smaller openings, with minimum-area requirements of ≤0.23 ha and optimal area values of ≤0.49 ha. The minimum area requirement for chestnut-sided warbler was not identified because the predicted probability of occurrence never fell below 0.5, while indigo bunting and prairie warbler exhibited greater area-sensitivity. Prairie warblers were the most area-sensitive species that occurred frequently enough in openings to be modeled, with an estimated minimum-area requirement of 1.11 ha. The results of the study have significant management implications; in situations where the goal is to accommodate all species in this study, the study found that land managers should consider creating openings >1.1 ha in size openings. However, in scenarios where this is not feasible, openings 0.23 ha in size can still provide habitat for several species of high conservation concern and openings 0.7 ha in size provide optimal habitat for all species but prairie warbler.

PACT uses equations derived from these empirical abundance-opening area relationships to calculate probabilities for 7 species (black-and-white warbler, chestnut-sided warbler, common yellowthroat, eastern towhee, gray catbird, indigo bunting, and prairie warbler). Because prairie warblers were shown to be influenced by the presence of adjacent large openings in Roberts and King (2017), PACT users can specify any large openings (clearcut > 5 ha or powerline corridor > 50 m wide) within 3km of the management opening to adjust prairie warbler opening area occupancy probabilities accordingly. The remaining 15 species of shrubland birds are assigned an occupancy probability function from the most similar species identified in Roberts and King (2017), and are classified into area-sensitivity groups based on data from published literature and professional judgement by PACT's development team and consulting stakeholders.
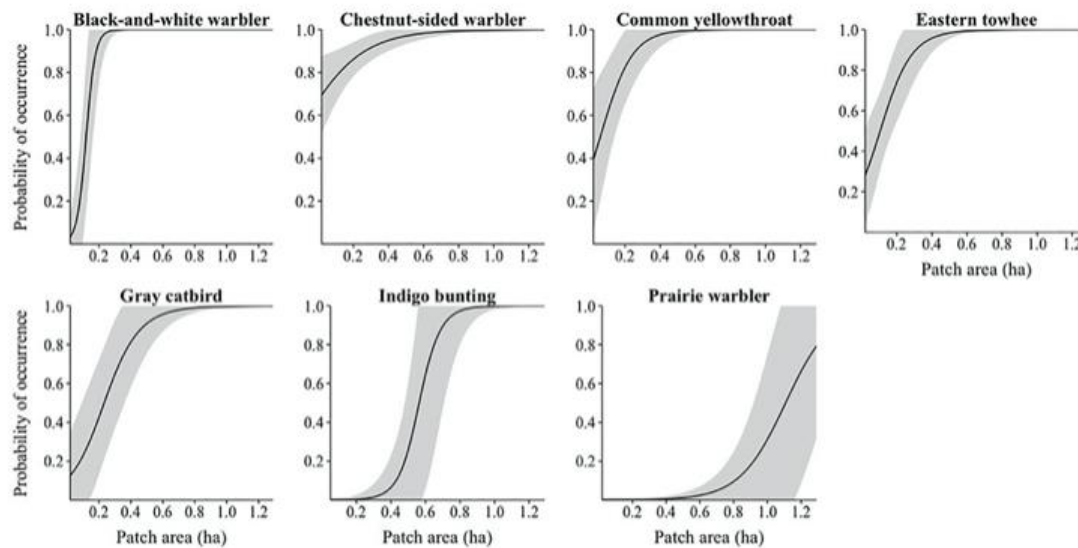
Figure 3. From Roberts and King (2017). The probability of occurrence of shrubland birds in relation to forest opening size in Western Massachusetts, USA, 2014 and 2015. Shaded areas representing 95% confidence intervals.

By incorporating this study's quantitative relationships and related qualitative assessments into PACT, land managers can easily use these findings to inform management decisions about opening area size in any location across Massachusetts, particularly when group selection harvests are being considered in lieu of even-age management options like clearcuts.

2. <u>Residual Basal Area:</u> A meta-analysis of the effects of tree retention on shrubland birds, by Akresh et al. (2021)

Akresh et al. (2021) conducted a meta-analysis based on data from 34 studies that examined the effects of silvicultural treatments on bird communities to provide a quantitative assessment of species-specific responses to tree retention levels along a gradient of stand conditions. The study examined shrubland bird densities as a function of three common management regimes: regeneration harvests with low retention (clearcut and seed-tree methods), regeneration harvests with moderate retention (shelterwoods), and high retention management regimes (commercial thinning, selection methods, and no management). The meta-analysis found that nearly all shrubland bird species were less abundant or absent from forests with high levels of canopy cover, thus indicating that that unmanaged forests, single-tree selection, and commercial thinning regimes are not recommended for shrubland bird management. Shrubland bird abundance can be achieved by the creation of open-canopy, early-successional forests via regeneration harvests; short-rotation maintenance of open-canopy habitats; creation of partially open canopy forests via silviculture; and the maintenance of partially open-canopy woodlands in fire-dependent ecosystems through prescribed burning and other related practices, where appropriate. Clearcuts and seed tree harvests were found to be the most effective for creating shrubland bird habitat, while variable retention harvest systems with live-tree legacies at densities <25% may also be an effective strategy. Furthermore, some species had equally high densities in stands with moderate tree retention of 30–70%, which supports the general use of retention forestry approaches. This

meta-analysis synthesized information for forest managers regarding how shrubland bird densities respond to tree harvesting practices, both along a continuous gradient of tree removal and at discrete intervals.

Three models were compared for each species: 1) a null model depicting constant density (without a predictor variable); 2) a model with a linear predictor of tree retention; and 3) a model with a quadratic and linear predictor of tree retention. The parameters from the best-supported model for each species are used to calculate the occupancy probability for residual basal area, but due to insufficient data, the parameters from a comparable species are used for brown thrashers and golden-winged warblers. The tool also provides a table (below) outlining recommended residual basal area values for shelterwood or selective logging systems in square feet per acre.

Forest Type	Shelterwood	Single-tree & Group Selection	Sources
Northern hardwoods	30-80	60-80	Leak et al 2014
Oak-hickory (Central hardwoods)	60-90	Not recommended	Gingrich 1971 Johnson et al 2011
Northern hardwoods/Mixed woods (Hardwoods & conifers)	30-80	100-110	Leak et al 2014
White pine	50-80	Not recommended	Lancaster 1984 Leak and Lamson 1999
Pitch pine	20-50	Not recommended	NJPC 2006

3. Time Since Treatment: Postlogging succession and habitat usage of shrubland birds by Schlossberg & King (2009) and Management regime influences shrubland birds and habitat conditions in the Northern Appalachians, by Smetzer et al. (2014)

The relationships in temporal changes in shrubland bird abundance following silvicultural harvests were quantified for PACT using data collected from Smetzer et al. (2014) and data collected from and reviewed in Schlossberg and King (2009). Schlossberg and King conducted a meta-analysis to determine how shrubland bird populations in the eastern United States respond to succession in the first 20 years after a timber harvest. Due to the variety of methods used to estimate avian abundance across studies, Schlossberg and King could not convert all results to the same measure, and therefore transformed observations from each study into a 0-1 scale by dividing each abundance value by the maximum abundance per species in that study. The results of the meta-analysis were used to estimate the effective area occupied by birds as a proportion of peak density in successional forests, thus estimating occupancy by substituting space for time in each species' graph of successional trends. With these results, the authors used the area under the abundance-time regression curves to estimate the proportion of regenerating forest used by each bird species. According to the outcome of the meta-analysis, many shrubland birds are stage-specific in their use of regenerating forests, with overall density and diversity peaking around year 10 in regenerating clearcuts. By year 20, shrubland birds are mostly replaced by mature forest birds.

Expanding upon these findings, Smetzer et al. systematically sampled birds over a successional gradient in both silvicultural openings and wildlife openings maintained by burning and mechanical treatment. Only openings <1 ha in area that were between 1- and 15-years post treatment were surveyed for each management type. After conducting point counts and completing surveys of vegetation structure and composition, statistical analyses showed that time since treatment was a strong predictor of bird abundance. Because this was the first study to sample systematically over a gradient of stand ages in early successional habitats created through

activities like silviculture, prescribed burning, and mechanical treatment, it offered new insight into management outcomes across a wider range of treatment types and stand ages. The data on how bird abundance changed with time since treatment gives managers the necessary information to accurately weigh tradeoffs between management options and to predict the impact of these choices on bid abundance.

In order to incorporate the findings of these two studies into PACT, the relationship between temporal changes and shrubland bird abundance was determined by comparing three models for each species: 1) a null model depicting no change in abundance over year since treatment; 2) a model with a linear predictor of year since treatment; and 3) a model with a quadratic and linear predictor of year since treatment. The parameters from the best-supported model for each species are used by the tool to calculate occupancy probabilities for time since treatment. However, due to insufficient data we use alternative approaches for the American goldfinch, blue-winged warbler, and brown thrasher. As obligate shrubland birds, these species were assumed to be absent from sites at 0 and >20 years since harvest and are therefore assigned the chestnut-sided warbler function. Data were lacking for two species, so functions were approximated as follows: white-eyed vireos are assigned the common yellowthroat function based on results from Perry and Thill (2013) and Twedt and Somershoe (2009). Lastly, because yellow-billed cuckoos are not considered sensitive to time since treatment (Perry et al., 2018), they are assigned an occupancy probability of 1 for PACT.

Final Occupancy Score and Additional Outputs

The final occupancy score generated by PACT (see Figure 2) is calculated as the product of regional occupancy and habitat occupancy probabilities. PACT also retrieves the Regional Concern Score (breeding season) (RCS-b) value from the Partners In Flight (PIF) database for each shrubland bird species included in the tool. PIF developed a system of prioritizing bird species in North America on the basis of their demography in multiple categories, which can be used to focus management efforts on the species most in need (Nuttle et al., 2003). These categorical scores are useful for deriving a priority rank per species that reflects the risk of local extirpation and can be used as species weights in an index to compare bird communities' conservation values overall (Nuttle et al., 2003).

The final occupancy and RCS-b values are dependent on the Bird Conservation Region (BCR) in which the management opening occurs. For openings that overlap multiple regions, values are taken from the region covering the greatest proportion of the opening. An empty cell indicates that there is no RCS-b score for the species in question in that BCR. The product of the final occupancy and PIF score for each species is also summed over all species. The formula is based on a modification to equation 1 in Nuttle et al. (2003) in which species occupancy probability is substituted for abundance (ai).

$$CV = \sum_{i=1}^{s} a_i w_i \qquad (1)$$

Incorporating Functions into PACT

After the functions in PACT were derived from the analyses performed by Roberts and King (2017), Akresh et al. (2021), Smetzer et al. (2014), and Schlossberg and King (2009), the function parameter values were incorporated into callable JavaScript functions specific to each shrubland bird species included in the tool. The species occupancy plots that are generated by the tool were created by calling the appropriate function over the viable range of the parameter of interest, while the initial point on the graph, represented as a black dot, was calculated from the 'Add Management Opening' specification. The adjusted point on these plots, represented with a red or green dot, was calculated from the current value on the associated slider (see Figure 4).
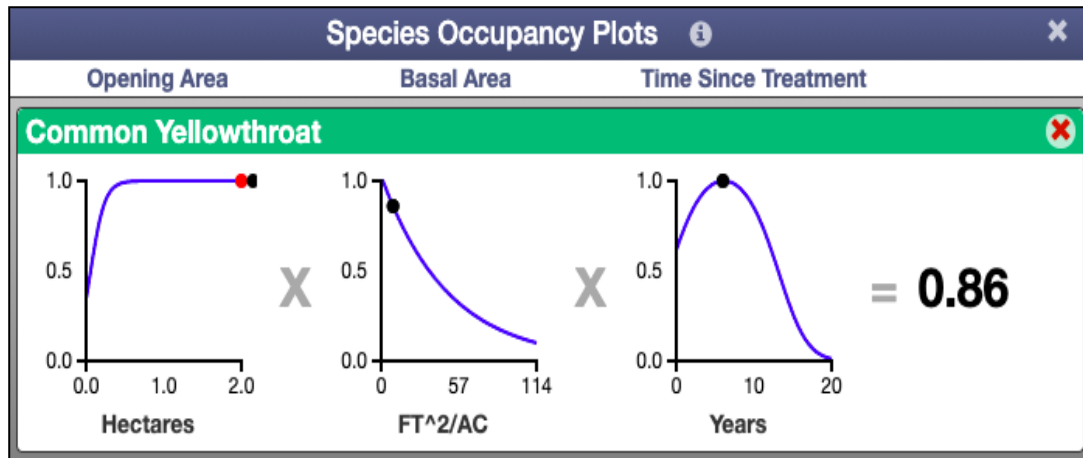
Figure 4. Example of species occupancy plots generated by PACT.

Development Process

The following flowchart (Figure 5) illustrates the various stages of development and feedback involved in bringing PACT to completion.

Figure 5. Flowchart of development process

Illustration of Functions
The following figures demonstrate the outputs of expected bird communities across Massachusetts generated by PACT.

1) The Northern Berkshires, MA

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
Common Yellowthroat	1.00	0.99	13	
American Goldfinch	0.96	0.87	11	
Chestnut-sided Warbler	0.94	0.86	14	
White-throated Sparrow	0.78	0.55	13	
Cedar Waxwing	0.96	0.52	11	
Blue-winged Warbler	0.55	0.50	12	
Eastern Towhee	0.93	0.47	13	
Gray Catbird	1.00	0.41	13	
Song Sparrow	1.00	0.40	13	
Indigo Bunting	0.82	0.33	8	
Canada Warbler	0.53	0.32	18	
Dark-eyed Junco	0.70	0.28	12	
Field Sparrow	0.84	0.27	12	
Black-and-white Warbler	0.93	0.25	15	
Alder Flycatcher	0.87	0.24	11	
Prairie Warbler	0.59	0.18	13	
Nashville Warbler	0.15	0.13	12	
Brown Thrasher	0.50	0.12	14	
Yellow-billed Cuckoo	0.07	0.07	10	
Mourning Warbler	0.05	0.03	13	
Golden-winged Warbler	0.03	0.01	13	

Adjusters ℹ

Opening Area ⟳	Basal Area ⟳	Time ⟳
0 — 1 — 2	1 — 58 — 114	0 — 10 — 20
Hectares	FT^2/AC	Years

Conservation Value of management opening ℹ **97.90**

🖼 Info & images of silvicultural treatments   ⬇ Download Results

2) The South Shore, MA

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
Common Yellowthroat	0.99	0.85	14	
American Goldfinch	0.87	0.72	11	
Chestnut-sided Warbler	0.79	0.72	14	
Gray Catbird	0.99	0.43	12	
Eastern Towhee	0.94	0.42	16	
Song Sparrow	0.99	0.36	12	
Cedar Waxwing	0.65	0.33	9	
Yellow-billed Cuckoo	0.31	0.31	14	
Blue-winged Warbler	0.30	0.25	18	
Alder Flycatcher	0.73	0.22	8	
Indigo Bunting	0.54	0.22	9	
Brown Thrasher	0.56	0.17	15	
Field Sparrow	0.47	0.16	15	
Prairie Warbler	0.50	0.16	17	
Black-and-white Warbler	0.57	0.15	14	
Nashville Warbler	0.10	0.08	12	
White-throated Sparrow	0.11	0.07	11	
White-eyed Vireo	0.10	0.03	12	
Canada Warbler	0.04	0.02	16	
Golden-winged Warbler	0.02	0.01	14	
Mourning Warbler	0.01	0.01		

Adjusters ℹ

Opening Area ⟳	Basal Area ⟳	Time ⟳
0 — 1 — 2	1 — 58 — 114	0 — 10 — 20
Hectares	FT^2/AC	Years

Conservation Value of management opening ℹ **74.02**

🖼 Info & images of silvicultural treatments   ⬇ Download Results

Figure 6. A comparison of outputs between a 1ha opening in 1) the Northern Berkshires, MA, and 2) in the South Shore, MA. The species likely to occur in each management opening are arranged in descending order of occurrence, with an overall conservation value for each opening appearing at the bottom of the window

Two years since treatment
Ten years since treatment

Figure 7. A comparison of the same 5 ha opening, two years vs. ten years post-treatment. Time since treatment was adjusted using the sliders in the Adjusters section of the window.

0.1 ha Opening

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
American Goldfinch	0.99	0.91	11	
Chestnut-sided Warbler	0.92	0.65	14	
Common Yellowthroat	1.00	0.61	14	
Song Sparrow	1.00	0.41	12	
Cedar Waxwing	0.94	0.31	9	
Yellow-billed Cuckoo	0.24	0.24	14	
Eastern Towhee	0.94	0.23	16	
Blue-winged Warbler	0.24	0.22	18	
Gray Catbird	1.00	0.09	12	
Black-and-white Warbler	0.62	0.06	14	
Nashville Warbler	0.06	0.05	12	
Canada Warbler	0.02	0.01	16	
Alder Flycatcher	0.84	0.00	8	
Brown Thrasher	0.46	0.00	15	
Dark-eyed Junco	0.01	0.00	8	
Field Sparrow	0.41	0.00	15	
Golden-winged Warbler	0.00	0.00	14	
Indigo Bunting	0.89	0.00	9	
Mourning Warbler	0.01	0.00		
Prairie Warbler	0.26	0.00	17	
White-eyed Vireo	0.02	0.00	12	

Adjusters

Opening Area — 0 ... 1 ... 2 Hectares
Basal Area — 0 ... 13 ... 26 M^2/HA
Time — 0 ... 10 ... 20 Years

Conservation Value of management opening — 49.13

Info & images of silvicultural treatments | Download Results

1.0 ha Opening

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
Common Yellowthroat	1.00	1.00	14	
American Goldfinch	0.99	0.91	11	
Chestnut-sided Warbler	0.92	0.83	14	
Cedar Waxwing	0.94	0.51	9	
Eastern Towhee	0.94	0.48	16	
Song Sparrow	1.00	0.41	12	
Gray Catbird	1.00	0.40	12	
Indigo Bunting	0.89	0.35	9	
White-throated Sparrow	0.39	0.28	11	
Alder Flycatcher	0.84	0.24	8	
Yellow-billed Cuckoo	0.24	0.24	14	
Blue-winged Warbler	0.24	0.22	18	
Black-and-white Warbler	0.62	0.16	14	
Field Sparrow	0.41	0.13	15	
Brown Thrasher	0.46	0.10	15	
Prairie Warbler	0.26	0.08	17	
Nashville Warbler	0.06	0.05	12	
Canada Warbler	0.02	0.01	16	
White-eyed Vireo	0.02	0.01	12	
Dark-eyed Junco	0.01	0.00	8	
Golden-winged Warbler	0.00	0.00	14	

Adjusters

Opening Area — 0 ... 1 ... 2 Hectares
Basal Area — 0 ... 13 ... 26 M^2/HA
Time — 0 ... 10 ... 20 Years

Conservation Value of management opening — 81.05

Info & images of silvicultural treatments | Download Results

Figure 8. A 0.1 ha opening compared to a larger, 1.0 ha opening at the same location. While the predicted species composition is similar at the site, the conservation value is significantly greater in the 1.0 ha opening.

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
Common Yellowthroat	1.00	1.00	13	
American Goldfinch	0.96	0.87	11	
Chestnut-sided Warbler	0.89	0.81	14	
Alder Flycatcher	0.81	0.72	11	
Field Sparrow	0.71	0.71	12	
White-throated Sparrow	0.71	0.51	13	
Cedar Waxwing	0.90	0.49	11	
Eastern Towhee	0.90	0.46	13	
Song Sparrow	1.00	0.41	13	
Blue-winged Warbler	0.44	0.40	12	
Gray Catbird	1.00	0.40	13	
Prairie Warbler	0.38	0.37	13	
Brown Thrasher	0.50	0.36	14	
Indigo Bunting	0.87	0.34	8	
Nashville Warbler	0.28	0.24	12	
Black-and-white Warbler	0.82	0.22	15	
Canada Warbler	0.34	0.21	18	
Yellow-billed Cuckoo	0.18	0.18	10	
White-eyed Vireo	0.12	0.12		
Dark-eyed Junco	0.25	0.10	12	
Golden-winged Warbler	0.09	0.08	13	

Adjusters

Opening Area — 0 | 1 | 2 Hectares
Basal Area — 0 | 13 | 26 M^2/HA
Time — 0 | 10 | 20 Years

Conservation Value of management opening: 110.88

Info & images of silvicultural treatments | Download Results

Species likely to occur in project area (in descending order of occurrence)

Species	Regional Occupancy	Final Occupancy	PIF Score	Graphs
Common Yellowthroat	1.00	1.00 -0.65	13	
American Goldfinch	0.96	0.87 -0.42	11	
Chestnut-sided Warbler	0.89	0.81 -0.29	14	
Alder Flycatcher	0.81	0.72 -0.43	11	
Field Sparrow	0.71	0.71 -0.38	12	
White-throated Sparrow	0.71	0.51 -0.35	13	
Cedar Waxwing	0.90	0.49 -0.21	11	
Eastern Towhee	0.90	0.46 -0.28	13	
Song Sparrow	1.00	0.41 -0.24	13	
Blue-winged Warbler	0.44	0.40 -0.19	12	
Gray Catbird	1.00	0.40 +0.09	13	
Prairie Warbler	0.38	0.37 -0.25	13	
Brown Thrasher	0.50	0.36 +0.08	14	
Indigo Bunting	0.87	0.34 -0.05	8	
Nashville Warbler	0.28	0.24 -0.09	12	
Black-and-white Warbler	0.82	0.22	15	
Canada Warbler	0.34	0.21 -0.05	18	
Yellow-billed Cuckoo	0.18	0.18	10	
White-eyed Vireo	0.12	0.12 -0.07		
Dark-eyed Junco	0.25	0.10	12	
Golden-winged Warbler	0.09	0.08 -0.05	13	

Adjusters

Opening Area — 0 | 1 | 2 Hectares
Basal Area — 0 | 13 | 26 M^2/HA
Time — 0 | 10 | 20 Years

Conservation Value of management opening: 110.88 -45.82

Info & images of silvicultural treatments | Download Results

Figure 9. The same 5.0 ha opening with no basal area compared to ~12.5 ha^2 of basal area, adjusted using the slider for Basal Area in the Adjusters section of the window.

Assessing PACT Based on Best Practice Recommendations (McIntosh et al. 2011)
The U.S. Forest Service strives to improve the delivery of high quality, relevant research and services to managers and stakeholders (Stout et al., 2007). PACT is a product of this organizational goal, reducing the research-implementation gap by synthesizing data and functions from relevant and recent primary literature into an accessible decision-making framework to guide management. As an open-source, web-based tool based on data and functions derived from peer-reviewed publications, PACT also offers its users the benefit of consistent access, a usable format, and credible information, which are all necessary elements to transcending the knowledge-action boundary (Cash et al., 2003). Furthermore, given the controversial nature of even-age management practices like clearcutting in the northeast, DSS can play a critical role in improving the transparency of decision formulation and solution for land managers interested in creating early-successional habitat for shrubland birds (McIntosh et al., 2011).

However, these attributes do not necessarily guarantee success or longevity for PACT; although DSS are perceived to have significant value in informing natural resource management, these tools often fail to be adopted by the intended end users due to challenges of engagement, adoption, and business, cost, and technology, and evaluation (McIntosh et al., 2011). Therefore, in order to assess the relative successes of PACT and to identify areas of improvement for future modifications, the tool's development process and attributes have been examined against a series of best practice recommendations produced by McIntosh et al. (2011). Best practice categories produced by this study include design for ease of use; design for usefulness establishing trust and credibility; promoting EDSS (Environmental Decision Support Tools) for acceptance; plan for longevity; and starting simple and small.

Design for Ease of Use
To design a DST for ease of use, McIntosh et al. (2011) recommends a user-friendly interface based on elucidating the user's needs and capabilities. This interface should be adaptable to different user types and should provide adequate help facilities. PACT was designed to be accessible to all users with access to a reliable internet connection, and who are familiar with standard map-based systems. The tool is specifically designed to accommodate the needs of decision makers like land managers and foresters who live and work in the state of Massachusetts, with language tailored to those with an understanding of silviculture and general forest resources management. To improve the user experience, a guided tutorial is provided on the welcome page. However, PACT is not currently developed for use with mobile devices and therefore is not designed to be accessible in the field. If additional assistance is required by the user beyond the tutorial, relevant contact information is provided in the Project Overview tab.

Design for Usefulness
McIntosh et al. (2011) suggests the roles, responsibilities, and needs of end users/stakeholders be identified at the beginning of the process to ensure a tool is designed for usefulness – a recommendation that was met by PACT in its nascency. Dedicated time and resources for a requirement analysis or usability survey are also recommended, along with the inclusion of social scientists to provide input regarding human factors. PACT accomplishes the identification of end users and their roles, responsibilities, and needs through the integrated development process and the clear language in the Welcome page. However, the limited resources of the development team have not yet allowed for input from social scientists regarding the tool's design. In lieu of this suggestion, feedback from practitioners including a forester affiliated with

Massachusetts DCR, an ornithologist for Mass Audubon, and a private service forester was used to guide modifications. This meets the recommendation within this category to work with end users and stakeholders to define project success. Future modifications will take into account the specific feedback provided by a larger group of foresters, which will further improve PACT's design for usefulness.

Establishing Trust and Credibility
The first recommendation within this category calls for openness and honesty about system weaknesses and areas in need of improvement, including model uncertainties and assumptions. One of the primary objectives of this paper is to achieve this very goal, specifically by comparing the tool to McIntosh et al. (2011) best practice recommendations in this section of the publication to foster transparency with users. Examining model uncertainties and assumptions within PACT is particularly relevant for this section, given the assumptions and substitutions that were made while incorporating data and functions from published literature into the tool. For example, the calculation for opening area required the classification of all bird species included in the tool into area-sensitivity groups. 15 species were classified into groups based on data from published literature and professional judgement and were assigned an occupancy probability function from the most similar species in Roberts and King (2017). This applied to five species (alder flycatcher, field sparrow, and white-eyed vireo, which were grouped based on data from Schlossberg & King (2007), golden-winged warbler, grouped based on data from Askins (1993), and the brown thrasher, based on professional judgement by David King.

An additional consideration relevant to this category is the predictive aspect of PACT. The information provided by an effective DST must be specific enough to generate estimates, or predictions, for end users that guide decision-making. However, it is critical that these predictions are realistic and reflect the "known unknowns" for a given scenario. PACT therefore aims to provide users with robust information, without presuming a level of detail not possible to achieve based on available data. For example, while focal shrubland bird species have been shown to occupy different niches within forest succession, the full details surrounding habitat use and selection currently exceed the capacity of PACT. Although the information in PACT is based on specific studies relating to shrubland bird habitat use based on factors like opening area, residual basal area, and time since treatment, environmental variables like soil moisture are not captured in these functions. Acknowledging the complications surrounding the predictive aspect of PACT is critical to building trust and credibility for the tool moving forward.

Promoting EDSS for Acceptance
In its current stage of development, PACT is preparing for beta-testing and its official release. Therefore, the best practices within this category can be used to maximize the acceptable and uptake of the tool moving forward. The first suggestion provided by McIntosh et al. (2011) is to find a champion to promote PACT at different levels of the organization. For the Northern Research station, this recommendation has already been achieved due to the composition of the development team. However, future efforts will be made to ensure that additional champions across both the policy and technical staff at the U.S. Forest Service will be identified to better meet this goal. Another recommendation for promoting EDSS for acceptance includes building capacity within the end user and stakeholder community. This will be met during the beta-testing phase of PACT, during which practitioners will be gathered at an in-person forum to review the tool. These stakeholders will be encouraged to help build capacity within their respective organizations. The final recommendation, which states that strategies should be implemented to

ensure DSS are easy and inexpensive to use, have already been achieved through PACT's open access, web-based interface.

Plan for Longevity
The plan for longevity for the PACT tool is a subject that merits additional consideration and improvement. McIntosh et al. (2011) recommends that planning in the early stages should consider the long-term use of the tool, including provisions for support and the adaptability of the tool to incorporate new data and information, or to be applied to new problems. In its current stage, the PACT development team does not have a documented plan to incorporate new data and information to the tool, which could put the tool's longevity at risk. However, it should also be noted that the U.S. Forest Service Northern Research Station has a stated commitment to long-term engagement in maintaining and improving any products the organization develops. Within this category of best practices McIntosh et al. (2011) also suggests that developers design a DSS that can be used to solve multiple environmental problems. In its current formulation, PACT is limited to silvicultural operations within New England, but the inclusion of shrubland bird species from other regions, and other forms of shrubland habitat management such as mowing or prescribed burns, are anticipated for future versions of the tool. Of note, PACT was not developed with the intention of solving multiple environmental problems, but rather to provide a specific decision-making framework to aid the creating and maintenance of early-successional habitat for shrubland birds in New England.

Starting Simple and Small
The final category of recommendations created by McIntosh et al. (2011) involves the incremental development of tools using known technology, the avoidance of undue model complexity, and the use of a modular approach to modelling frameworks. PACT has been in development since 2016, thus meeting the recommendation of incremental development. Additionally, the technology used to build PACT is well-known and avoids undue complexity, keeping the tool generally "simple and small."

Conclusion
This set of recommendations published by McIntosh et al. (2011) was written to stress the importance of understanding user needs, being clear about the purposes of a given DST, the importance of a collaborative relationship between developers and practitioners/stakeholders, and the building and maintenance of credibility and trust. Interestingly, the findings of this study indicated that the success of use of a tool was more closely related to the development process than the end product. Therefore, despite the areas of improvement identified for some of the best practice recommendations listed above, PACT's collaborative, user-oriented development process and foundation of trust indicate that this DST is likely to experience successful adoption and longevity in the conservation space.

As a DST, PACT is well-positioned to enable managers to create and maintain early-successional habitat to help conserve shrubland bird species in New England. This decision-making framework effectively synthesizes the management implications produced by the published literature on shrubland birds, facilitating the dissemination of information to managers in a usable, credible, and accessible format. In addition to achieving this critical goal, PACT's participatory and iterative development process can be used to inform the creation of future conservation decision support tools.

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V. Presentations, workshops, and publications

Presentations:

1. Akresh, M., King, D., Coombs, J., Nislow, K., Ritterson, J., and J. Collins. April 2018. An early-successional shrubland habitat decision support tool. Northeast Association of Fish and Wildlife Agencies Conference, Burlington, VT.
2. Akresh, M., King, D., Coombs, J., Nislow, K., Ritterson, J., and J. Collins. April 2018. An early-successional shrubland habitat decision support tool. Northeast Natural History Conference, Burlington, VT.
3. Akresh, M., D. I. King, J. A. Coombs, K. H. Nislow, J. D. Ritterson, C. A. Lott, J. L. Larkin, and J. Collins. April 2019. A meta-analysis of the effects of tree retention on shrubland bird densities: from clearcuts to unharvested forest. Northeast Association of Fish and Wildlife Agencies Conference, Groton, CT.
4. McInvale, S. L., Akresh, M., and D. I. King. August 2020. A meta-analysis of edge effects on nest success in forest and shrubland birds of eastern North America. North American Ornithological Conference.
5. M. Akresh, D. King, and S. McInvale. June 2021. A Meta-Analysis of the Effects of Tree Harvesting on Shrubland and Forest Birds. Northern Hardwoods Conference 2021.

Workshops:

1. Ritterson, J., Fish, J. and King, D. May 6, 2021. Invitation – Help test decision-support tool that describes the benefits of forestry to shrubland birds. Webinar.

Publications:

1. McInvale, S.L., M.E. Akresh and D.I. King. *In Prep*. A meta-analysis of edge effects on birds.
2. Akresh, M.E., S.L. McInvale, D. I. King, C. J. L. Larkin and A. W. D'Amato. *In Prep*. Effects of tree harvests on mature-forest bird species and forest-shrubland bird communities in eastern North America: A Meta-analysis
3. Akresh, M.E., D. I. King, C. A. Lott, J. L. Larkin and A. W. D'Amato. 2021. A meta-analysis of the effects of tree retention on shrubland birds. Forest Ecology and Management 483:118730.

IV. Errata

We were able to accomplish the purpose of this agreement to "develop tools that will inform management of habitat for mature-forest and shrubland birds", including the tradeoffs between habitat management for mature forest and shrubland birds. It turned out, however, that the incorporation of some of the demographic and habitat variables increased the complexity of the bird habitat models, and furthermore, was impractical given the paucity of published information. For this reason, we retained patch size and area-related abundance, but omitted interspersion because it was not practical to expect landowners to quantify this metric. Similarly, there was insufficient information on postfledging habitat selection and habitat-specific survival at the species level to model it meaningfully. Conversely, we were able to provide detailed information on the influence of harvest intensity on both mature forest and shrubland birds through a meta-analysis of published information, a component that was not included in the original scope, which greatly enriched the final product, a decision support tool that describes the influences of silviculture on shrubland birds. Work was delayed on incorporating mature forest birds into the decision-support tool, although the models describing the response of these species to harvest intensity based on the meta-analyses are complete, and the distribution maps have been obtained from our collaborators. This final stage of the development of the decision-support tool will be underway early in 2022.